UNDERSTANDING PATTERN-PROCESS RELATIONSHIPS IN A HETEROGENEOUS LANDSCAPE: EFFECTS OF LARGE TERMITARIA ON DIVERSITY AND DISTURBANCE REGIMES IN MIOMBO WOODLANDS OF NORTHERN ZIMBABWE

Grant Stuart Joseph

Percy FitzPatrick Institute, DST-NRF Centre of Excellence

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Thesis presented for the degree of Doctor of Philosophy

Grant Stuart Joseph

Percy FitzPatrick Institute, DST-NRF Centre of Excellence

Department of Zoology

University of Cape Town

Rondebosch

7701

South Africa

Supervisors:

Professor Graeme S. Cumming,

Percy FitzPatrick Institute of African Ornithology, University of Cape Town

&

Professor David H.M. Cumming,

Percy FitzPatrick Institute of African Ornithology, University of Cape Town & Tropical Resource Ecology Programme, Department of Biological Sciences, University of Zimbabwe

Submitted: March 2012

DECLARATION

This submission contains original research undertaken towards a Ph.D. degree in Zoology at the University of Cape Town's Percy FitzPatrick Institute. The work is my own, and to the best of my knowledge contains no material previously published by another person, except where specifically acknowledged within the body of the text. As aspects of Chapter 6 have been published (citation: Joseph, G.S, Cumming, G.S, Cumming, D.H.M., Mahlangu, Z., Altwegg, R. and Seymour, C.L. 2011. Large termitaria act as refugia for tall trees, deadwood and cavity-using birds in a miombo woodland. Landscape Ecology. 26:439-448), specific co-author contributions are qualified within the acknowledgements.

Grant Stuart Joseph

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Signed by Candidate

Signature Removed

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I dedicate this thesis to:

My father, **Peter Joseph** who always took the time to show me the wildest places he could find. Such a privileged childhood has filled a certain aspect of my mind with an enduring appreciation for the intricacies of life.

My mother, **Val Hardman** (nee Van der Spuy), who gave me the freedom to play in a garden that led to a valley of herps, mammals and arthropods. I have not forgotten the snakes 'n snails that you allowed into our house, or the frequent visits to the Port Elizabeth Museum, Snake Park and 'tropical hothouse', which were probably not every fashionable woman's first choice of destination in the summers of the seventies.

My colleague, **Zacheus Mahlangu**. The privilege of working with you in Chizarira will always be remembered. You walked me calmly from the centre of a pride of lions at a time when I'd almost lost the wherewithal to think (let alone move). You taught me the names of every miombo plant. You single-handedly scared off a group of poachers and their dogs, armed only with wise words. But most importantly, it was through you that I learned the true meanings of two words: 'dignity' and 'respect'.

Abstract

Spatial heterogeneity has been shown to influence ecosystem processes and important ecosystem properties like resilience and biodiversity, allowing species with specific habitat needs or weaker competitive abilities to persist in disturbed systems that might otherwise have excluded them. Miombo covers 2.7 million km^2 and is Africa's largest savanna woodland. Much of this is characterized by *Macrotermes* termitaria, which can be hotspots of both plant (primary) productivity and animal abundance (secondary and tertiary productivity). To investigate the modulating influence of spatial heterogeneity in the form of large *Macrotermes* termitaria on woody plant and avian diversity in the face of herbivore impacts and fire (the two disturbances most amenable to management), research progressed in stages.

First I investigated the role of soils and mound surface area in the development of unique woody plant assemblages that characterize termitaria. Distinct, mound area-related assemblages emerged in relation to surface area and soil nutrients; indicator trees from the matrix dropped from mound assemblages, to be replaced by mound indicator species, at area-related intervals. Establishment of mound-associated trees from biomes beyond the dystrophic woodland resembled savanna tree patch dynamics. Such increased structure has in other studies been shown to attract avians and herbivores (mounds can be feeding hotspots), enhancing nutrient and propagule deposition (from beyond the woodland matrix), and adding niches to the system.

As ecosystem processes are driven by the functional traits of individual species and their interactions, different suites of woody plant species (as found on termitaria) can be expected to make different contributions to ecosystem function. The relationship between fine-scale spatial variation in community composition and system function was explored by considering how spatial heterogeneity associated with termitaria within a heavily elephant-impacted miombo woodland influences the functional traits represented within the woody plant community. Termite mounds harboured species with response functional groups different to matrix species, connoting a system better equipped to handle disturbances, providing an example of how fine-scale spatial heterogeneity that fosters alpha diversity, can also influence functional diversity.

Given that browsing and mixed feeding are known to decrease woody cover, and that *Macrotermes* termitaria can be repositories for tall woody trees, a study of the influence of mounds and different herbivore treatments (browsing vs. grazing and mixed feeding vs. exclusion over a 40 year period) on woody plant assemblages and functional diversity revealed: (1) mound-based woody plant assemblages are more similar to one another than to matrix-based assemblages, regardless of herbivory; (2) type of herbivory leads to different woody plant assemblages between mounds, and the same finding applies to matrix plots; (3) mounds enhance functional diversity, harbouring higher functional richness than matrix plots; (4) functional richness decreases with exposure to browsing; and (5) maintenance of functional evenness with lowered functional richness reveals a community contracting in trait space by loss of similar functional types across treatments, connoting lowered functional resilience.

At finer scales, local heterogeneity can add complexity to fire regimes. By examining the fire-sparing effect of large termitaria on woody plant structure and composition, it emerged that termitaria, with significantly lower grass cover, and with vegetation at higher elevations than the surrounding matrix, represented refugia from fire for plant species with poor adaptation to fire that might otherwise have been excluded from the system.

By harbouring habitat favoured by cavity-using birds (tall trees, trees with deadwood, and cavities) in elephant-impacted woodland, greater termitarium density correlated with greater species richness and abundance of cavity-using birds. Mounds emerged as refugia (driven primarily by increased on-mound deadwood), contributing to persistence and resilience of this functionally important guild.

Macrotermes termitaria emerge as important repositories for unique woody species, and through their amelioration of the disturbance regimes of fire and herbivory, they contribute directly to the diversity of both woody plant species and woody plant functional diversity, which in turn enhances the diversity of avian guilds dependant on such habitat. As regional populations continue to burgeon, and as land-use for both agriculture and settlement intensifies, the identification of patterns and processes that harbour biodiversity and potentially add resilience to the miombo woodland system becomes increasingly important.

Acknowledgements

Edward O. Wilson in 1984 described biophilia as not merely the love of nature, but an "*innate tendency to focus on life and lifelike processes*". And it is biophilia that Alfred Russel Wallace expresses more than a century ago, when he describes a new species of birdwing butterfly on Bacan Island in the Malay Archipelago. "*The beauty and brilliancy of this insect are indescribable, and none but a naturalist can understand the intense excitement...On ... opening the glorious wings, my heart began to beat violently, the blood rushed to my head, and I felt much more like fainting than I have done when in apprehension of immediate death. I had a headache the rest of the day, so great was the excitement produced by what will appear to most people a very inadequate cause".* To those of us who derive emotional reward and fulfilment through nourishing this aspect of spirit and mind so interwoven into our human consciousness, there is a certain privilege attached to living in a true wilderness.

And so the satisfaction of completing this thesis must be balanced by the closure of a period that has given me a platform from which to enjoy the charm and subtle artistry of a miombo woodland and its processes. It is difficult to express the contentment that comes with living for months in such an isolated and biological intricate wilderness. I thank my supervisors Graeme and David Cumming firstly for having the faith to allow me this opportunity, at a time when logistical challenges often appeared insurmountable. Not only did they offer me support within Zimbabwe (which involved detailed planning for officially sanctioned research, and the solutions to everyday complications such as the procurement of fuel; no easy task when none is available!). They have also provided firm academic guidance and a fresh approach to latent ideas, and at the same time have offered me the scope to pursue my own interests. I thank them too for their constant availability for critical comment.

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Aspects of Chapter 6 were published in 2011 (citation: Joseph, G.S, Cumming, G.S, Cumming, D.H.M., Mahlangu, Z., Altwegg, R. and Seymour, C.L. 2011. Large termitaria act as refugia for tall trees, deadwood and cavity-using birds in a miombo woodland. Landscape Ecology. 26:439-448), and the contributions of each party were as follows: I collected the data, analysed, interpreted and wrote the paper. Colleen Seymour and Zacheus Mahlangu contributed to collection of the data. Res Altwegg provided statistical input that included advice on most appropriate method of analysis, which I then undertook and interpreted. David and Graeme Cumming, as supervisors of the chapter, offered guidance in both literature searches and methods of data collection. David Cumming furthermore offered advice on data collection methods in the field. Graeme Cumming provided fruitful ideas that were developed further.

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1

Introduction

In recent years, ecology has seen a growing level of interest in understanding how spatial heterogeneity influences ecosystem processes and important ecosystem properties like biodiversity, disturbance regimes and resilience. Spatial heterogeneity acts at a variety of scales to influence population structure, community composition and ecosystem processes (Pickett and Cadenasso 1995). It can influence biodiversity through, *inter alia*, effects on survival and growth rates (Beckage and Clark 2003), dispersal success (Howe and Smallwood 1982, Valiente-Banuet et al. 1991), resource availability (Ettema and Wardle 2002b) and disturbance regimes (Clarke 2002). Spatial heterogeneity also causes natural disturbances to act heterogeneously in landscapes, because physical features and vegetation influence the frequency, severity and type of disturbance within patches (Turner 1989). It can impact on a wide range of ecological dynamics. For example, spatial heterogeneity in resources and/or perturbation regimes can modify predator-prey interactions (e.g., Kareiva 1987); can create opportunities that allow species with specific habitat needs or weaker competitive abilities to persist in a system (e.g., Bakun and Broad 2003); and can result in the formation of localised feedback loops between landscape structure and ecological communities (reviewed in Cumming et al. 2008).

Most studies addressing spatial heterogeneity have focused on systems with an asymmetrical arrangement (e.g., responses of plant communities to elevation gradients) or in which habitat patches are surrounded by an inhospitable matrix (e.g., metapopulation models). Less attention has been given to situations in which there are strong interactions between patch and matrix, or in which the importance of patch composition becomes gradually more marked as matrix quality declines. Such situations are common in ecosystems where patches that are small relative to the home range of a species contain high quality resources. Examples include springs, salt licks, abandoned (but nutrient-enriched) cattle enclosures (Young et al. 1995), and even the spatial distribution of soil organisms (Ettema and Wardle 2002a), which can affect distribution and diversity of plant species (Huston and De Angelis 1994).

A striking example results from the foraging activity of the mound building *Macrotermes* (Isoptera) termite. The termite genus *Macrotermes* (Macrotermitinae) occurs in the Afrotropical and Oriental regions The 12 African species are distribution in habitats ranging from rain forest to arid savannas (Ruelle 1970, Uys 2002). *Macrotermes* mounds generally occur at densities of 2-4 mounds/colonies per hectare (Lee and Wood 1971). They are the largest of all termites, building epigeal nests containing a subterranean fungus-comb cavity. Their mounds, up to 9 m high and 30 m in diameter (Lee and Wood 1971), are a prominent feature of many African and Indo-Malayan landscapes (Wood and Sands 1978, Desanker et al. 1995) and may occupy more than 5% of the land surface area (Holdo and McDowell 2004). Colonies may contain up to 200 000 termites (Meyer et al. 2000). The diet of *Macrotermes* consists of dry grass, leaf litter, herbivore faeces and dead wood. They have two feeding modes. The one is direct feeding on plant matter. The other involves feeding on *Termitomyces* fungus combs (Hinze et al. 2002) to which they feed their faeces, with different worker casts specialising on different feeding modes. Instead of remaining merely a food source as they are in other genera of the Macrotermitinae (Hyodo et al. 2003), the fungi associated with *Macrotermes* break down lignin, enhancing effective use of cellulose(Hyodo et al. 2000).

Density estimates of *Macrotermes* termitaria vary widely (Lepage 1984, Meyer et al. 2001), averaging around 1-4/ha over large areas (Pomeroy 1977).Temporal population dynamic of *Macrotermes* remain poorly understood, partly because aging of colonies is difficult. Colonies that build mounds may die out, but mounds may be re-colonized by the same or different species, and broken mounds may be repaired (Cadet et al. 2004), with varying rates of mound erosion occurring during occupation and desertion. Consequently, mound size and occupation are poor indicators of both mound and colony age. At any one time it appears that around 20-50% of mounds are inactive; in Uganda the number of unoccupied mounds varied from 21% for *M.*

subhyalinus to 42% for *M. bellicosus* (Pomeroy 1977), whereas in the northern Kruger National Park in South Africa it was as high as 53 % for termites of which the dominant genus was *Macrotermes* (Meyer et al. 1999). Mortality rates vary from year to year (Lepage 1984), with predation by Aardvark *Orycteropus afer* and Doryline ants (Hymenoptera: Formicidae, Dorylinae) being important in some areas, and varies with colony age (Darlington et al. 1992). Large mounds in this study were documented as being dormant or active, and there was no significant difference regarding vegetation composition or soils between dormant and active termitaria.

Macrotermes concentrate nutrients and increase biomass of degraded organic matter at mounds (Pomeroy 1976, Collins et al. 1984), often leading to relative impoverishment of the surrounding matrix (Jones 1989). Mound soils can have a higher moisture content (Watson 1969, Weir 1973, Dangerfield 1991) and greater infiltration capacity than adjacent soils (Abbadie and Lepage 1989, Traoré et al. 2008). They accumulate carbonates (which raises pH; Watson 1967, Konaté et al. 1999) and contain high levels of organic matter (through termite foraging) which in the presence of cellulose-decomposing fungi within the mounds, enhances nutrient cycling. As calcium, potassium, phosphorus, nitrogen and magnesium generally occur at elevated concentrations on mounds (Lopez-Hernandes et al. 2006), they can be considered as eutrophic hot spots (Hesse 1955, Watson 1969, Jones 1989, Jones 1990, Frost 1996, Loveridge and Moe 2004), with higher biodiversity (e.g., Wild 1952, Fleming and Loveridge 2003) than the surrounding, generally dystrophic, woodland (Huntley 1982).

Macrotermes termitaria harbour a distinct woody plant assemblage relative to the woodland matrix (Fanshawe 1968, Fleming and Loveridge 2003). They provide important foraging resources for large ungulates (Holdo and McDowell 2004, Loveridge and Moe 2004, Mobæk et al. 2005) and megaherbivores (most notably elephant) are attracted to trees which on mounds can have elevated leaf nutrient content (Ruggerio and Fay 1994, Holdo 2003). Herbivore litter resulting from increased grazing and browsing attention is also added to the nutrient cycle by termite foraging (Holdo and McDowell

2004). Consequently, mounds of the Macrotermitinae subfamily also emerge as foci for vertebrate taxa such as cavity-using birds (Joseph et al. 2011) and small mammals (Fleming and Loveridge 2003), certain reptile species, and invertebrate diversity, thus elevating primary, secondary and tertiary productivity (Pringle et al. 2010). As patches of enhanced soil fertility have greater impact in low nutrient systems, effects on woody plant assemblage and structure can be expected to be marked (Scholes 1990, Belsky and Canham 1994, Mobæk et al. 2005). This study specifically addresses the effects of termite-constructed nutrient rich islands in nutrient-poor soils, on woody plant species and functional diversity, in the context of two important disturbances regimes, herbivory and fire.

Although the quantification and qualification of biodiversity can reasonably be traced to the origins of taxonomy itself, the foundations for our current framework emerged relatively recently. Franklin et al. (1981) saw biodiversity as having three primary attributes: composition, structure and function. Noss (1990) expanded this to a nested hierarchy incorporating elements of each into four levels of organisation that encompass different spatio-temporal scales: regional landscape, community ecosystem, population-species and the finer genetic level. Walker (1992), in an effort to address the difficulties of attaining conservation management goals in the face of inadequate resources, suggested that a sensible start to minimising species loss would be to maintain the integrity of ecosystem function. If biodiversity is taken to be the integration of variability, spanning scales that range from the level of nucleotides and genes, to the broader scale of species, and through to course spatial measures such as ecosystems and landscapes, then functional groups with little redundancy might warrant priority conservation effort. Nested within this reasoning was the concept that ecosystem resilience (the ability of a given system to maintain processes and structure despite perturbation; Holling 1973, Walker et al. 2006) is increased by greater species richness. Although the literature is rich in commentary of how structural diversity and compositional diversity interplay (Pimm 1984, Walker 1995, Bellwood et al. 2003), the concept of functional diversity remained a relative latecomer.

The past decade has seen an increased focus on the links between functional diversity and its effect on compositional and structural diversity (Tilman et al. 1997, Tilman 2001). Diaz and Cabido (2001)

highlighted an emerging consensus that functional diversity (that is, the value and range of species traits), as opposed to species richness per se, can strongly determine ecosystem function. A greater appreciation of function soon led to the emergence of the principle of functional redundancy, 'the degree to which organisms have evolved to do similar things' (Rosenfeld 2002), and an expectation that overlap of function might contribute to increased resilience (the ability of a given ecosystem to adapt to change through maintenance of function; Elmqvist et al. 2003)

My study sites in the miombo woodland of south-central Africa represent the southern aspect of a dystrophic savanna system that extends through central Zimbabwe, Angola, Mozambique, Zambia, the Democratic Republic of the Congo and Tanzania. These southern deciduous woodlands are interspersed with islands of nutrient-rich patches in the form of *Macrotermes* termite mounds. Dynamics of miombo woodland are governed by edaphic factors and long-term climate cycles, with short-term oscillations being driven by seasonal rainfall, fire, herbivory and anthropogenic impacts. The influence of herbivory (and its intimate associations with fire regimes) and man are the two variables most amenable to management. Anthropogenic change can be contained by regional governmental policy; fire and herbivory fall within the scope of reserve managers.

In miombo, as with other woodland systems, the synergy between intensive elephant herbivory and fire can result in the conversion of woodland to grassland or shrubland that largely lacks tall trees (Cumming et al. 1997, Mapaure 2001, Mapaure and Campbell 2002). Reductions in tree canopy cover can lead to increases in grass biomass. Grass provides fuel which can subsequently support hotter fires (Mapaure 2001, fig. 1.1), leading in turn to the potential for alternate stable states (Westoby et al. 1989, Starfield et al. 1993). Working in miombo woodland, Thomson (1974) tracked the growth of trees, and postulated that elephant and fire accounted for a loss of 20% of trees per annum from his study site. By 1981 his predictions had proved to be correct; the woodland in question had disappeared (Cumming 1981). Comparison of historic with contemporary photographs, and studies of aerial photographs from neighbouring Sengwa Wildlife Research Area (which showed a decrease in miombo woodland cover from 95.2% in 1958 to 68.2% by 1996; Mapaure and Campbell 2002) support these earlier findings.

Figure 1.1. High grass cover provides a substrate for dry-season fires when elephant open up the woodland canopy

Over the past century, elephant numbers south of the Kunene and Zambezi rivers have increased from less than a few thousand to over 250 000 (D.H.M. Cumming pers. com.) In the miombo woodlands of Zimbabwe, one consequence has been the transformation of the structure of the woodland, and an increase in regenerating and converted trees (tall trees broken to form shrubs, fig. 1.2.).

Controversy remains as to whether elephant facilitate the maintenance of biodiversity through the creation of new niches (Dublin et al. 1990, Herremans 1995) or whether they decrease biodiversity by habitat degradation (Conybeare 1989, Dublin et al. 1990, Hall-Martin 1990, Cumming et al. 1997). In either case, however, the more general role of spatial heterogeneity in maintaining biodiversity and providing resilience within elephant- and fire-dominated systems system is poorly understood.

An important aspect of my study sites is their differing exposures to herbivory. High elephant densities at certain sites (and the associated influence that this can have on fire regimes), and a gradient of ungulate herbivory at other sites, provide an opportunity for testing whether the fine-scale spatial heterogeneity associated with termitaria contributes to more general (and broad scale) ecosystem functional diversity, biodiversity and resilience by providing refugia for key functional elements of the system as matrix quality declines in the face of disturbance.

Figure 1.2. Chizarira National Park, with trees converted by elephant herbivory

My study investigates the influence of spatially explicit patches (in the form of termitaria) on woody plant biodiversity, functional diversity, and diversity of a guild of birds with specific woody plant habitat needs, in a setting of the foraging effects of herbivores and elephants at densities above those known to change woodland to grassland (Cumming 1981, Dunham et al. 2006). To ascertain the extent to which the landscape heterogeneity created by the prominent ecosystem engineer (the *Macrotermes* termite) influences the system, I focus on the following core questions:

1) How do unique woody plant assemblages form on termitaria?
2) Do termitaria harbour woody species with functional traits that differ relative to matrix species and if so, does this influence functional diversity of the woodland in the context of high densities of a second prominent engineer (*Loxodonta africana*, the African Elephant)?

3) Are there differences between on and off-mound woody plant assemblages and functional groups across a gradient of ungulate herbivory, and if so what implication does this hold for woodland functional diversity?
4) Do termitaria act as refugia from fire for woody plant species, and does the selective pressure of fire influence the observed differences between woody plant species on mounds and in the woodland matrix?
5) Do mounds harbour preferred habitat for cavity-using birds, and what consequences might this have for diversity and resilience for this guild of birds?

To this end, the timing of this study of miombo woody species (following 3 decades of high elephant densities for my western study sites in Chizarira National Park, and 40 years of exposure to differing herbivore impacts at my eastern study sites) is opportune, as it provides sufficient time to examine for effects of disturbance (fire and herbivory) and fine scale heterogeneity on biodiversity and functional diversity of woody plant species. This research has been driven not only by scientific endeavour. It has taken place at a difficult juncture in the history of life (a mass extinction of species), and as such has been inspired too by a need to better identify areas, patterns and process that might add species and functional diversity to the system in question.

Humans now number 7 billion. With the erosion and disappearance of the migration routes of old, reserves increasingly resemble islands. The consequent loss of range for wild ungulates and megaherbivores has resulted in transformation of many protected areas (Ben-Shahar 1998, Eckhardt et al. 2000, Holdo 2003), and within south-central Africa this matter has become a prominent concern for managers and conservation biologists. The situation has been compounded by the knowledge that for Africa (and Latin America) protected areas may actually attract people, who then settle in the surrounding land at almost double the average rural growth rate for a given region (Wittermeyer et al. 2008). More intensive land-use practices have already resulted in the rapid and ongoing transformation of miombo systems (Campbell et al. 1996), a situation unlikely to reverse given current trends. Indeed, since 2007 I have witnessed the growth of a nearby village (by almost five kilometres in radius) so that it now abuts

upon the boundary of Chizarira National Park. Historic buffer zones of the reserve have over a decade become populated at densities that reflect permanent settlements (fig. 1.3).

Figure 1.3. Land abutting on the Chizarira National Park boundary. Grassless soils reflect fields that have been ploughed for crops; the remaining grass is grazed by cattle.

By necessity I have maintained a conservation focus, aiming to provide knowledge that might improve not only our understanding of the links between heterogeneity and biodiversity, but that also assists managers and conservationists in identifying ecologically important processes and habitats. This study examines how spatial heterogeneity and disturbance regimes (herbivory and fire) can facilitate additional niches for plant and bird communities. Beyond the research itself, it is hoped that this work might contribute to improved custodianship, and sustainable management of miombo systems, and in so doing avoid the scenario under which an important empirical question arises: at what point do such systems lose their buffering capacities, and what might be the trophic consequences of such an outcome?

General outline of the thesis

Each chapter is structured as an individual paper. This has resulted in the repetition of some introductory information (particularly with regard to termitaria). Where feasible, methods are only repeated if necessary. Of relevance at the beginning of this thesis is a note on the limits of this study. To address the full impacts of the effects of termite mounds on biodiversity and their influence on disturbance regimes in this woodland system would entail a detailed look at effects across a broad range of taxa, and an examination of ecological patterns and processes at a variety of scales. The scope of this research is necessarily limited to the questions that aroused my immediate curiosity. Nevertheless, it still captures the spatial influence of large *Macrotermes* mounds, and the disturbance regimes of herbivory and fire, on the diversity of the system, within the restricted context of woody plants and cavity-using birds. Although findings have implications for both the resilience of miombo woodlands and the guild of birds in question (cavity-users), their implications for resilience are inferred from the directly quantified findings on biodiversity and functional diversity, and resilience itself has not been directly measured.

Chapter 2 investigates the effects of both mound surface area and soil composition in explaining the observed woody plant species community differences that exist between mound and woodland matrix. Previous studies have demonstrated a difference between matrix and mound plant assemblages, which has generally been ascribed to changes in soils (composition and water content) through the effects of termite foraging (Fleming and Loveridge 2003). I sampled mounds of areas ranging from 0.36 m^2 to 1220 m^2, and tested the effect of mound surface area and soil composition on woody plant assemblages and species richness; and whether the establishment of such assemblages can be similar to the establishment of woody species in the subcanopy patches beneath savanna trees (sensu Belsky et al. 1989, Dean et al. 1999).

As functional diversity, as opposed to biodiversity per se, can strongly determine ecosystem function (Díaz and Cabido 2001), Chapter 3 examines differences in woody plant functional groups on mounds and in the woodland matrix. Consideration is given to overlap of function, which can be expected to contribute to increased resilience (Elmqvist et al. 2003). Any increase in woody plant functional

diversity as a consequence of the presence of termitaria can be expected to have important consequences for overall function of the woodland, particularly in the context of high megaherbivore foraging pressure.

Chapter 4 addresses the effects that different exposure to herbivory (grazing vs. browsing and mixed feeding vs. exclusion) has on woody plant assemblage and functional diversity, and examines for differences not only between sites, but within sites on and off termitaria. As termitaria are nutrient hotspots with a unique suite of trees, they might behave differently relative to the matrix woodland, following 40 years of differing herbivore pressures.

Chapter 5 examines whether large termitaria provide a refuge from fire for woody plant species that grow upon them. Large termitaria can have relatively increased soil moisture, and their structure often elevates the base of trees above the level of flames. Increased fire exposure in the matrix, and more marked fire adapted responses like resprouting, would suggest that woody plants in the matrix are fire adapted (Nefabas and Gambiza 2007). I postulate that if this were to be the case, then mounds, in acting as refugia for trees ill-adapted to the local fire-regime, might be providing a niche for a suite of trees that could otherwise have been absent from the system.

Chapter 6 investigates the effect of termitaria and elephant on woody plant structure, and how this might influence cavity-using bird diversity. Cavity-using birds are dependent on tall, old trees with deadwood and cavities, for nesting and roosting (Newton 1994). A reliance on this habitat makes cavity-using birds potentially sensitive markers of woodland degradation. By testing whether such habitat is concentrated on mounds or in the matrix, and determining whether such factors influence cavity-using bird species richness and abundance, the influence of spatial heterogeneity as a consequence of ecosystem engineering by certain taxa (in this case termites and elephant) on a third group (cavity-using birds), is evaluated.

Chapter 7 is the concluding synthesis in which I summarise my findings, and evaluate the mechanisms and extent to which large termitaria influence disturbance regimes and diversity of woody plant species and certain avian guilds. These findings form the platform for future management

suggestions, and are further reflected upon with a view to addressing the scientific questions that new knowledge inevitably poses.

Comments on study site, data analysis and methods

A cursory description of the study site, and the many statistical techniques and methods common to more than one chapter, follows. Techniques specific and unique to a certain chapter are only described within that chapter. Those described here, and repeated within chapters, are reported again only if failure to do so would result in loss of clarity for the reader.

Study sites

Miombo is a broad leaved deciduous woodland dominated by the Caesalpinioideae genera of *Brachystegia* and *Julbernardia* (White 1983). In many parts of south-central Africa, miombo woodland is characterized by massive vegetated termitaria up to 9 m high and 30 m in diameter at the base (Malaisse 1978), which form nutrient-rich hotspots (Frost 1996). All study sites within Chizarira National Park and adjacent to Lake Chivero are dominated by such mounds which are possibly centuries old (Watson 1967), constructed by *Macrotermes* termites.

The study sites for investigating the effects of termitaria on woodland plant species assemblages, woody plant functional diversity, and diversity of cavity-using birds in the face of high elephant densities were situated in the Chizarira National Park in north-western Zimbabwe (fig. 1.4). Within the reserve, 3 discrete areas where sampled for the effects of fire; overall 102 mound-matrix pairs where surveyed. For the study on cavity-using birds, 25 plots where surveyed over different seasons, within which were nested the mound-matrix pairs. Specific sample size and design pertaining to each question is further qualified within the relevant chapter.

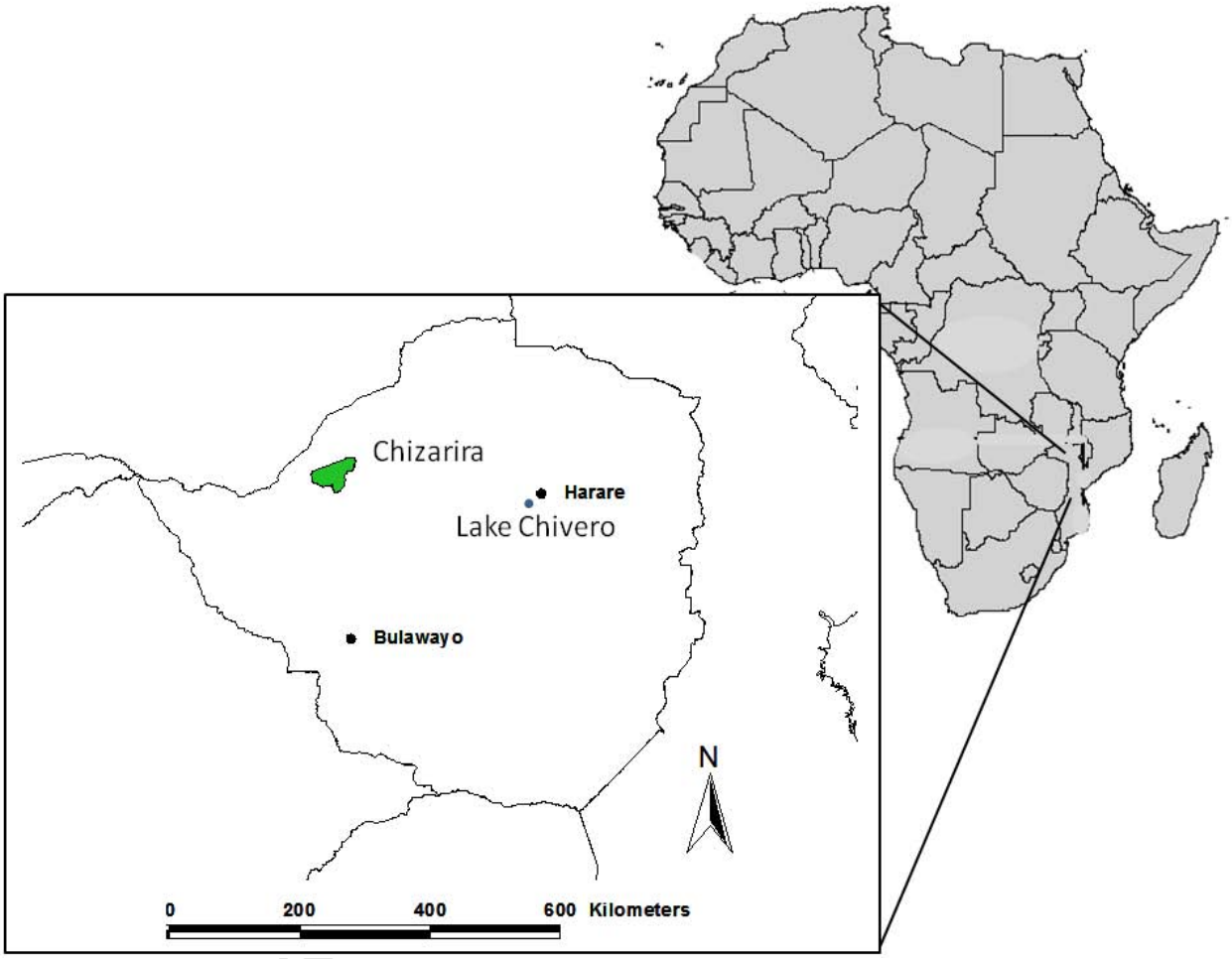

Figure 1.4. Schematic representation of study sites within Zimbabwe: Chizarira National Park (17°42´S, 27°55´E) is 192000 ha^2 in area, and harboured 25 sites for assessing cavity-using birds, 3 sites for testing fire effects on woody plants, and 149 mound-matrix sites. The sites adjacent to Lake Chivero (17°52´S, 30°46´E) included the Chivero Game Reserve, Bird sanctuary and Glen Roy farm, and encompassed a total of 40 mound-matrix sites.

The impacts of elephants and fire have transformed most of the park's former tall, open woodland to shrubland (Cumming 1981) comprised mainly of regenerating *Brachystegia boehmii* and *Combretum* species in the matrix, with tall trees being confined to termitaria (fig. 1.5).

Figure 1.5. In Chizarira National Park, tall trees persist on termitaria, whilst the woodland matrix harbours converted and resprouting trees.

Chizarira experiences a wet season from November to April, a cool dry season from May to July and a hot dry season from August to November. Mean annual temperature is 20 - 22.5°C (maxima: October 32.5-35°C, July 22.5-25°C; Torrance 1965). Mean annual rainfall is 600mm-800mm (annual coefficient of variation of 25-30%; Lineham 1965).

To determine the influence of termitaria and herbivory on woodland plant species assemblages, woody plant functional diversity and resilience, three adjacent sites within the miombo woodlands surrounding Lake Chivero in northern Zimbabwe (fig. 1.4), each with a different history of exposure to

herbivory, where compared. Two sites contained 15 mound-matrix pairs, and the third site contained 10 pairs. The 6100 ha Lake Chivero National Park is composed of a bird park (all large herbivores excluded), and a fenced game park of 1867 ha, containing browsers, mixed feeders and grazers. A fence separates the 650 ha Glen Roy farm (which contains grazers - Brahman cattle) from the bird park. The area experiences an average annual rainfall of 800 mm. Mean annual temperatures are 13° C (minimum) and 25° C (maximum; Torrance 1965).

Statistics and Methods

As every chapter required a specific analytical approach, the specific methods and statistical approaches are dealt with as they arise within each chapter.

Results of preparatory statistical tests have not been reported in the main text. Where necessary, data were tested both for normality and equality of variances prior to any parametric analyses being performed. A Shapiro Wilk's W test (Shapiro et al. 1968) was employed to assess any deviations from normality, and the residual scatter of parametric results was checked for homoscedacity.

Further information regarding Mann-Whitney, Wilcoxon, Kruskal-Wallis and Chi-square tests, and all multivariate techniques used, are elaborated upon in the relevant chapters, as are other methods of analysis, including post-hoc tests specific to certain questions. All analyses pertaining to functional trait data are qualified within the chapter specific to that topic.

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2

When termite mounds become islands: woody plant species assemblages relative to termitarium size and soil properties

Abstract

Macrotermitinae termitaria have emerged as hotspots for plant and animal diversity. When not dormant, they are dynamic structures varying in size and soil nutrient concentrations that harbour a unique woody plant assemblage. Instead of sitting like islands in an inhospitable matrix, they provide an example of a strong, dynamic interaction between patch (the termitarium) and matrix (in which the termites forage for nutrients that they concentrate within the termitarium). Given the well documented implications of area and patch dynamics to species composition, this study explores the sequence of changes in both soils and woody plant species and assemblages as mounds enlarge. Within a miombo woodland in north-western Zimbabwe, I compared woody plant assemblages on 43 matrix plots with 95 *Macrotermes* termitaria across a range of surface areas, using ANOSIM, cluster analysis and MDS ordination. I compared soil nutrients, pH and clay, from 10 large and 10 small termitaria, and 10 matrix sites. I also assessed how relative representation of large mound or matrix indicator species changed with mound area. Change was apparent even at > 10 m^2, where both soils and plant assemblages on mounds were significantly different to those of the matrix. Plant assemblages fell into two main groups at 20% similarity, the first comprised of matrix plots, mounds < 10 m^2 and some mounds between 10 – 30 m^2; the second, the remainder of the mounds between 10-30 m^2 and all mounds >30 m^2. At 40% similarity, four groups emerged: matrix, mounds <10m^2, mounds 10-30m^2 and mounds > 30 m^2. Woody plant composition changed gradually as mound area increased. On termitaria < 10 m^2, only 25% of indicators were mound indicator species, but on mounds between 10-30 m^2 in size, 62.5% were mound indicators. On termitaria over 30 m^2 in surface area, only mound indicator species were found. Through termite activities in concentrating nutrients and clay, termitaria provide habitat for species usually excluded from the matrix. The process of mound building and the nature of the plants that establish on them seems to set up a positive feedback for establishment of other non-woodland matrix species.

Introduction

Miombo woodland, which grows on dystrophic soils (Huntley 1982) and covers 2.7 million km^2, is Africa's most extensive savanna woodland formation. Vast areas characterized by *Macrotermes* (Isoptera) termitaria, house tree assemblages both different in composition and far taller in structure than the surrounding matrix. Historically Wild (1952) recorded more Capparaceae and Celestraceae on termitaria than in the surrounding matrix in a Zimbabwean woodland, and subsequent studies from south-central, east and western Africa confirm the presence of distinct and structurally taller assemblages of woody species on large termitaria (Glovers et al. 1964, Fanshawe 1968, Guinko 1984, Fleming and Loveridge 2003, Traoré et al. 2008, Moe et al. 2009). A growing interest in the ecological effects of Macrotermitidae has shown mounds to be foci for browsing (Holdo and McDowell 2004, Loveridge and Moe 2004), cavity-using birds (Joseph *et al.* 2011), small mammal diversity (Fleming and Loveridge 2003), arthropod and gecko abundance, and to thus increase primary, secondary and tertiary productivity (Pringle *et al.* 2010). Despite this, little focus has been drawn to the process of establishment and development of the distinct woody plant assemblages as small mounds enlarge into sizeable islands.

Patch dynamics (Levin and Paine 1974) can influence community assemblage, composition, and structure. For example, the development of nutrient-enriched patches beneath large and isolated savanna trees, following both altered nutrient cycling and increased animal activity, leads to fertile islands with plant communities distinct from the savanna matrix (Belsky and Canham 1994, Dean et al. 1999, Treydte et al. 2011). Many studies of the ecological relevance of spatial heterogeneity and its influence on biodiversity focus on systems in which patches of suitable habitat sit like islands within a matrix (e.g., Island Biogeography and metapopulation models). Fewer consider cases in which there are strong interactions between patch and matrix. Such situations are common in ecosystems where patches that are small relative to the home range of a species contain unique or high quality resources. Examples include salt licks, roosting sites, caves, freshwater springs, the nutrient-enriched areas of sites historically used for cattle enclosures (Young et al. 1995), and even the spatial distribution of soil organisms, particularly

those that affect nutrient cycling and decomposition (Ettema and Wardle 2002). Their arrangement can influence spatial patterning of plant species which become separated within patches, ultimately enhancing local diversity (Huston and De Angelis 1994).

Perhaps the most pertinent example in African savannas involves Macrotermitinae, the mound-building termites. Through enrichment of soils which are often mineral- and base-poor, they concentrate nitrogen, phosphorous, potassium, bases and elevate clay content, and their large termitaria emerge as topographically localized nutrient hotspots (Watson 1977, Malaisse 1978, Button et al. 1983, Frost 1996) with altered hydrology and drainage which can stimulate growth, diversity and composition of woody plant species (Hesse 1955, Fanshawe 1968, Wood and Sands 1978, Arshad 1982, Lal 1987, Jones et al. 1994, Schuurman and Dangerfield 1996, Dangerfield et al. 1998).

As patches of enhanced soil fertility have greater impact in low nutrient systems, effects on woody plant assemblage and structure can be expected to be marked (Scholes 1990, Belsky and Canham 1994, Mobaek et al. 2005). This study specifically addresses how matrix assemblages growing in nutrient-poor miombo soils dominated by the Caesalpinioideae genera of *Brachystegia* and *Julbernardia* (Malaisse 1978, White 1983, Millington et al. 1994) alter into distinct mound assemblages. It explores the sequence of changes in both soils and woody plants as mounds enlarge, and considers the influence of foraging by both termites and other taxa on tree recruitment, nutrient deposition and propagules dispersion as a consequence of increased vertebrate attention.

Given the importance of enriched soil patches, the consequences of tree establishment, and patch size, I consider principles from both savanna tree patch dynamics and island biogeography theory. Extending the prominent generalization in ecology that species number increases with increasing area to termitaria, the species-area relationship predicts that smaller patches will have lower diversity and species richness than will larger patches (MacArthur and Wilson 1967, Brown 1978), although this is not always so (Sulkava and Huhta 1998, Hodge et al. 2000). African savanna canopy trees can influence community assemblage, composition, and structure through the development of nutrient-enriched patches beneath large and isolated savanna trees. Large roots transport and concentrate nutrients; increased animal activity

influences nutrient cycling; and seed-dispersing vertebrates are drawn preferentially to such trees, adding woody species propagules (Kellman 1979, Canham 1988, Belsky et al. 1989, Belsky and Canham 1994, Dean et al. 1999). The resultant fertile islands of distinct plant communities influence local microclimate and resource availability (Belsky and Canham 1994, Dean et al. 1999, Treydte et al. 2011).

In testing the effect of increasing mound surface area on soil composition, woody plant assemblage composition, and species richness, I ask:

1) are small mound soils more similar to large mound, or to matrix soils, and does change occur even at small surface areas?

2) are changes in soils and surface area reflected by changes to woody plant assemblage, and does mound surface area influence woody plant species richness?

3) at what surface areas do (a) matrix species disappear (i.e. lose the ability to survive on mounds) and (b) new species colonize the mound (from non-miombo biomes)?

In addressing these questions, there is the possibility that a number of surface-area and soil-related assemblages exist en-route to establishment of a mature mound assemblage. If so, influences on niche availability and overall diversity can be anticipated.

Methods

Study site

This study was conducted in the miombo woodlands of Chizarira National Park (CNP), north-western Zimbabwe. Much of the park is characterised by patches in the form of large vegetated termitaria occurring at densities of $2ha^{-1}$ (Joseph *et al.* 2011), and as dispersal of propagules is more limited on isolated islands which contain fewer species (McArthur and Wilson 1967), it is noteworthy that large termitaria within the study were approximately equidistant. The area experiences a wet season from November to April, a cool dry season from May to July and a hot dry season from August to November. Mean annual temperature is 20 - 22.5°C (maxima: October 32.5-35°C, July 22.5-25°C, Torrance 1965).

Mean annual rainfall is 600mm - 800mm (annual coefficient of variation of 25-30%, Lineham 1965). Surveys were conducted in October 2007, April 2008 and November 2009. As the surveys included only perennial woody plant species, seasonal change had little impact on species presence/absence.

Field Methods

I surveyed a total of 95 mounds and 43 matrix plots, recording woody plant species. I estimated mound surface area by modelling mounds as cone-shaped. In an effort to compare equal areas (for matrix and mound), I sub-sampled 100m^2 of mound (selected by randomly choosing a compass bearing connecting the centre of the mound to its perimeter, and using this radius as the southernmost aspect of a pie-shape). Matrix plots were all 2 m x 50 m (100 m^2). Matrix plots were set along randomly chosen compass bearings radiating out from the large mounds (those with a diameter of > 10 m or height of > 2 m), starting 10 m from the perimeter of the mound. Mindful of both edge-to-area ratio when using sampling areas of differing shape, I nevertheless chose a long quadrat shaped plot to better represent matrix species occurring at a distance from the mound. The concern that a plot of such shape might also capture a greater amount of underlying soil and micro-topographical heterogeneity was minimised by selecting sites from areas with similar catenal position, altitude and distance from drainage lines. Mound surface areas ranged from 0.36 m^2 to 1220 m^2.

To compare patterns of soil nutrients for mounds of varying size and the woodland matrix, I collected soil samples from 10 matrix plots, 10 small and 10 large termitaria which represented a subset of the larger vegetation plot dataset. Soil samples of approximately 400g were collected at a depth of 0 – 20cm (Mills et al. 2009). Soil surface was loosened with a shovel, and then collected with a corer. Two samples were collected for each site, and the analyzed sample represented a composite of the two. Samples were air dried and sieved to <2 mm, digested in HNO_3 and H_2O_2 (EPA 2007) and analyzed for clay content, macro- ($N\text{-}NH_4$, $N\text{-}NO_3$) and micronutrients (calcium [Ca], potassium [K], magnesium [Mg], sodium [Na], boron [B], selenium [Se], molybdenum [Mo], cobalt [Co], iron [Fe], zinc [Zn], manganese [Mn], phosphorous [P] and sulphur [S]) by inductively coupled plasma atomic emission

spectrometry (Agilent 7500 ICPMS, Santa Clara, CA, USA). Electrical conductivity and pH where analyzed in 1:5 soil: water extracts. Analyses were carried out by the Agricultural Research Council in Pretoria, South Africa.

Statistical Analysis

Comparisons of soils between large and small mounds and the matrix

I constructed a dissimilarity matrix for the soils dataset, using Euclidean distance, and sorted the data using group-averaging. Data were standardised by dividing each matrix entry by its column total to enable comparisons of the divergent units of measurement of soil components and characteristics, namely pH, electric conductivity, macronutrient [N-NH_4, N-NO_3], micronutrient [Ca, K, Mg, Na, B, Se, Mo, Co, Fe, Zn, Mn, P and S] and clay content (PRIMER v. 6, Clarke and Gorley 2006). I then compared soil composition at different mound surface areas (< 10 m^2, 10 – 30 m^2, > 30 m^2, chosen from a pilot study of vegetation analysis on mounds, which showed alteration in woody tree species patterns for these areas), using an analysis of similarities (ANOSIM; Clarke and Green 1988). ANOSIM is analogous to an ANOVA for community similarities; it compares mean ranks of dissimilarities between groups and among groups (Clarke 1993). ANOSIM produces an R statistic, between -1 and 1, where a value of 0 indicates that the groupings are completely random.

Comparisons of woody plant assemblages between large and small mounds and the matrix

I used ANOSIM and multidimensional scaling to compare woody plant assemblages between matrix plots and large mounds. The nature of this study meant that some mounds were unavoidably smaller than 100 m^2. One option for comparing assemblages from samples of unequal size is to standardise the dataset by dividing each matrix entry by its column total and multiplying by 100. In this way, all samples have the same percentage composition of species, although information about total abundance is lost (Clarke and Warwick 1994). Although this method is statistically valid, and ensures that later analyses using the Bray-Curtis coefficient reflect differences in community composition, the loss of abundance information can be problematic, and smaller samples will unavoidably have fewer species. Furthermore, and possibly

more problematic, is that for the smallest mounds, species characteristic of those habitats might not be detected and consequently might be under-represented. I therefore used two statistical approaches to investigate differences in mound species composition with size (appendix 2.2).

In the first approach, I standardised the data by dividing each matrix entry by its column total to account for different sampling areas (woody plants abundance n = 7747, woody plant species n = 116) comprising 43 matrix plots, 38 large termitaria > 30 m^2, 30 mounds < 10m^2, and 27 mounds 10 – 30 m^2 in area (PRIMER v. 6, Clarke and Gorley 2006). I then examined differences in woody plant species assemblages by constructing a similarity matrix for the woody plant species dataset, using the Bray-Curtis similarity coefficient, sorting the data using group-averaging.

In the second approach, to try to account for the effect of species abundance of the smaller mounds, I compared them at equal area with the rest of the data set by randomly selecting a number of smaller mounds and summing them to a total surface area of 100 m^2, thus creating fewer, but more comparable, hypothetical small mounds. I ran this random selection procedure in R (R Development Core Team 2010). This was performed for all mounds with surface areas below 100 m^2. An alternative would have been to compare the vegetation of all mounds at areas equal to that of the smallest mound (0.36 m^2 in this study), which was not feasible considering that the basal areas of some of the larger single trees on large mounds were greater than this.

Using these two approaches, I examined differences in woody plant species assemblages between:

(1) the woodland matrix (n = 43) vs.

(2) small termitaria < 10 m^2 (n = 6 when random selection was employed to an area that sums to 100 m^2, comprised of random assemblages from 30 mounds under 10 m^2) vs.

(3) intermediate termitaria 10 – 30 m^2 (n = 9, from 27 mounds 10 – 30 m^2 in area) vs.

(4) large termitaria > 30 m^2 (n = 38)

by again constructing a similarity matrix for the woody plant species dataset, using the Bray-Curtis similarity coefficient, and sorting the data using group-averaging (PRIMER v. 6, Clarke and Gorley 2006). I plotted woody plant species richness against mound surface area, to examine the relationship between mound area and species richness.

To ascertain whether increasing mound surface areas excluded woody species characteristic of the matrix, and favoured those that characterize large mounds, I identified species that could be considered 'indicators' of the matrix, and large termitaria > 30 m^2. I did this using a method developed by Dufrêne and Legendre (1997), which considers a perfect indicator species to be always present in, and exclusive to that habitat, with scores ranging from 0 (no indicator value) to 100, using the statistical package PC-Ord. "Indicator values" are assigned to each species in each habitat, and the program then tests the null hypothesis of no difference between habitats using a Monte Carlo simulation, using 1000 randomizations. I then documented at which termitarium surface areas these individual species disappeared from, or colonised, mound-based woody communities.

Results

As noted, large termitaria generally have higher pH, electrical conductivity (EC), clay content, macro-micronutrient concentrations than the matrix. Study-site soil data supported the literature (table 2.1). I recorded a 70 fold increase in $N\text{-}NO_3$, a 30 fold increase in electrical conductivity, 19 fold for Na, 10 fold for Ca, 6 fold for B, 4 fold for Mg, 3 fold for K, and a doubling in clay content, and the macro-and micro-nutrients Se, Mo, Co, Cu, Mn, Zn and S.

Table 2.1. Comparative soil composition; matrix vs. very small (< 10 m^2) vs. small (< 30 m^2) vs. large termitaria (values expressed as $mg.kg^{-1}$).

Soil Variable	Matrix (value ± SD)	Small termitaria <10m^2	Intermediate termitaria 10-30m^2	Large termitaria >30m^2
pH	5.20 ± 0.33	5.30 ± 0.30	6.00 ± 0.96	7.52 ± 0.22*
EC	7.10 ± 1.97	11.80 ± 4.02	48 ± 67.50	254.90 ± 373.88*
Clay	12.00 ± 4.52	12.40 ± 3.23	17 ± 6.87	25.00 ± 6.20*
Ca	402.19 ± 103.1	538.85 ± 152.11	1241.38 ± 1127.82	4300.40 ± 600.02*
K	66.05 ± 29.14	232.13 ± 292.50	197.24 ± 200.52	229.83 ± 107.78*
Mg	74.02 ± 25.67	96.53 ± 29.78	141.08 ± 83.18	393.30 ± 84.38*
Na	5.18 ± 2.55	5.32 ± 2.84	7.21 ± 4.05	96.04 ± 79.26*
B	0.04 ± 0.01	0.05 ± 0.02	0.06 ± 0.01	0.26 ± 0.19*
Se	0.23 ± 0.20	0.17 ± 0.21	0.24 ± 0.19	0.38 ± 0.18*
Mo	0.03 ± 0.01	0.05 ± 0.04	0.05 ± 0.04	0.06 ± 0.05*
Co	4.54 ± 1.47	7.05 ± 3.42	7.26 ± 2.61	8.08 ± 2.10*
Cu	8.14 ± 13.03	8.83 ± 1.78	13.03 ± 06.39	20.21 ± 7.41*
Fe	10625 ± 2983	12423 ± 3694	14123 ± 4149	16580 ± 4022
Zn	28.11 ± 13.58	51.09 ± 28.09	57.98 ± 39.73	45.41 ± 19.15*
Mn	285.40 ± 43.89	264.34 ± 110.23	234.14 ± 83.40	511.30 ± 174.64*
$N\text{-}NH_4$	6.76 ± 0.50	13.11 ± 8.60	11.76 ± 6.38	7.38 ± 2.79
$N\text{-}NO_3$	3.07 ± 1.15	4.42 ± 1.48	25.97 ± 45.20	221.70 ± 320.94*
P	4.90 ± 3.69	9.42 ± 8.11	5.59 ± 6.91	3.28 ± 1.48
S	8.44 ± 1.05	5.35 ± 3.12	6.60 ± 3.36	15.12 ± 9.45*

* $p < 0.05$ (comparison of large termitaria vs. matrix)

Matrix soils clustered with those of small termitaria, suggesting similarity in soil composition. Large mounds formed a separate cluster (fig. 2.1).

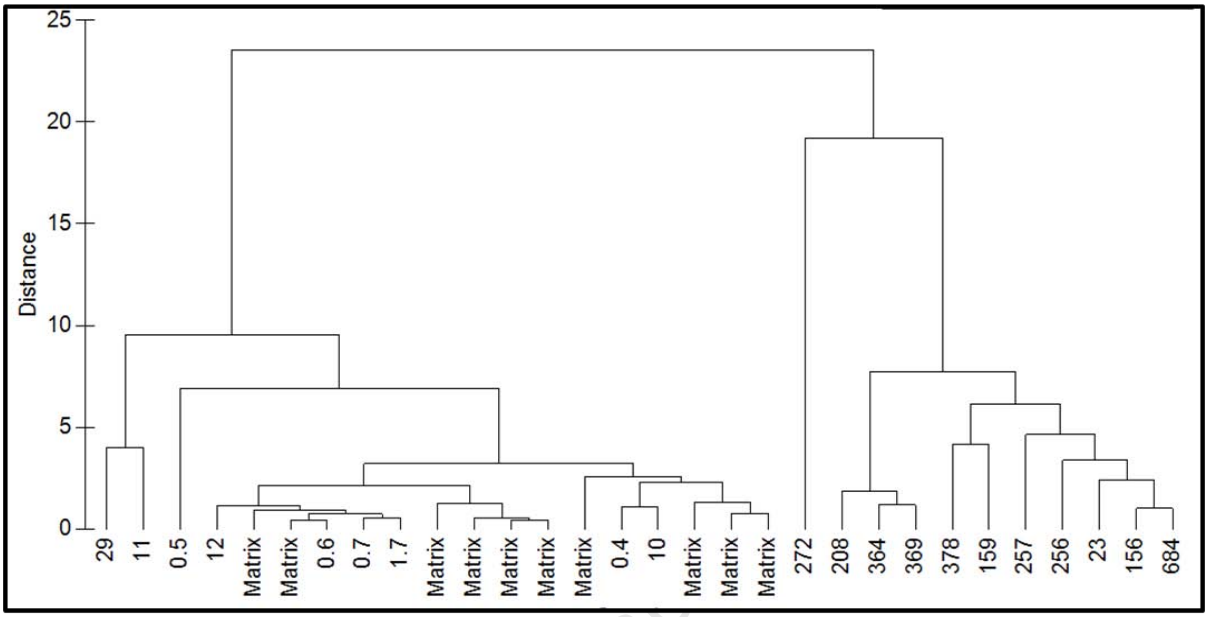

Figure 2.1. The dendrogram produced from cluster analysis demonstrates that soil composition differed between matrix and large termitaria. Numbers represented individual termitarium areas (m^2).

ANOSIM confirmed that no difference exists between soil composition of matrix and small mounds < 10 m^2. Matrix soils differed significantly from mounds of intermediate size (10 – 30 m^2), and larger mounds > 30 m^2 differed significantly with all soils groupings (table 2.2). Mounds of 10 – 30 m^2 in area emerged as distinct from both matrix and large mounds, but not from smaller mounds.

Table 2.2. ANOSIM comparing matrix, small, intermediate and large mounds for overall soil composition (Global R statistic = 0.563; p = 0.01)

Groups	R Statistic	Significance level p
matrix vs. mound < 10 m^2	0.081	0.247
matrix vs. mound 10- 30 m^2	0.505	0.008
matrix vs. mound > 30 m^2	0.948	0.001
mound < 10 m^2 vs. mound 10- 30 m^2	0.144	0.095
mound < 10 m^2 vs. mound > 30 m^2	0.909	0.001
mound 10- 30m^2 vs. mound > 30 m^2	0.424	0.010

As anticipated, species richness increased with increasing mound area (fig. 2.2).

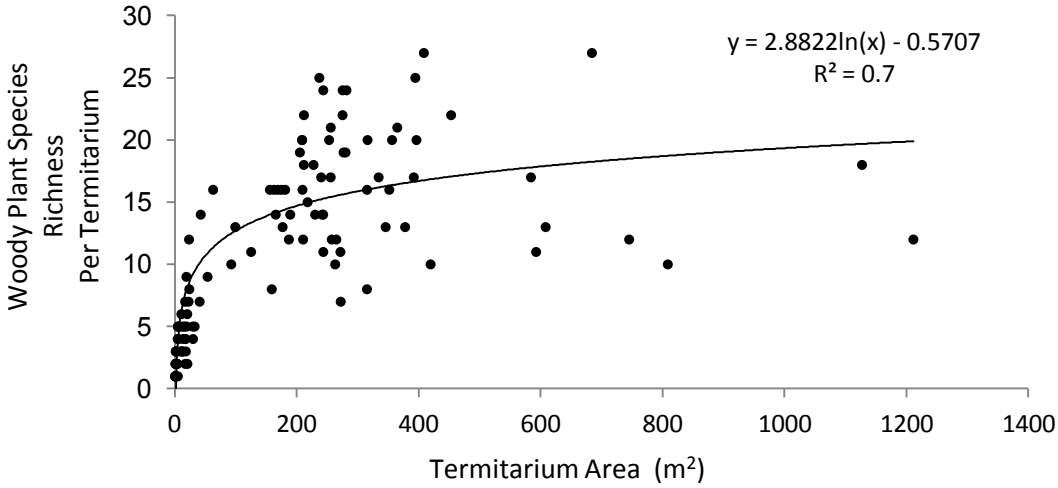

Figure 2.2. The relationship between woody plant species richness and termitarium area.

Multidimensional scaling (fig. 2.3) revealed that at broad levels of similarity (20 %), two core groupings emerged: (1) matrix sites, which clustered as a group with all termitaria < 10 m^2 and some termitaria 10 – 30 m^2 (2) large mounds > 30 m^2, which overlap with certain termitaria 10 – 30 m^2. At higher similarity (40 %), four groupings emerge: (1) matrix sites (with a large degree of overlap with mounds < 10 m^2), (2) mounds < 10 m^2, which associate closely to matrix sites, (3) mounds 10 – 30 m^2, with no similarity to matrix assemblages and (4) large mounds > 30 m^2. Imposing the results produced by the cluster analysis confirmed the groupings shown.

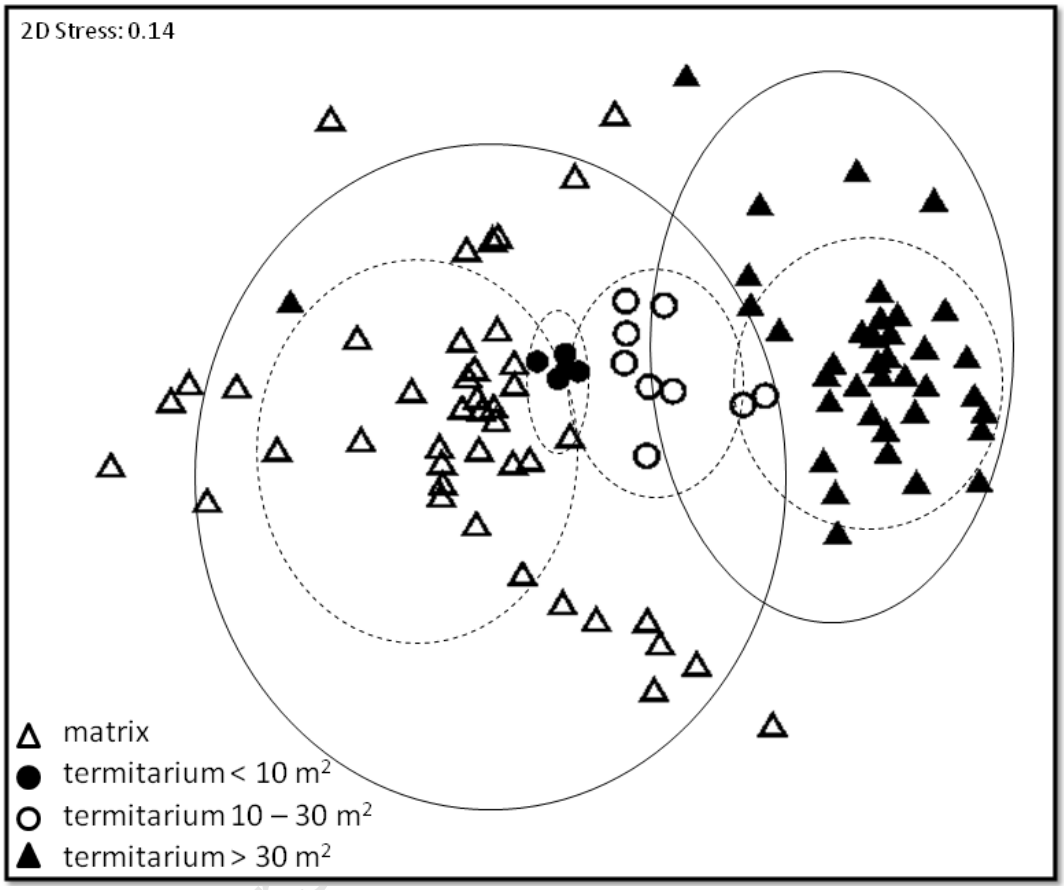

Figure 2.3. Ordination representing woody plant species assemblages for matrix vs. mounds of differing areas (< 10 m^2, 10 – 30 m^2 and > 30m^2). Solid circles represent assemblages similar by 20% or more; dashed groupings indicate similarities at 40%.

ANOSIM confirmed that no difference existed between matrix woody plant assemblages and those on small mounds, but at areas > 10m^2 a significantly different assemblage emerged, and another at > 30 m^2 (table 2.3).

Table 2.3. ANOSIM comparing matrix, small, intermediate and large mounds for woody plant assemblage (Global R statistic = 0.509, p = 0.001)

Groups	R Statistic	Significance level p
matrix vs. mound < 10m^2	-0.113	0.782
matrix vs. mound 10- 30m^2	0.169	0.046
matrix vs. mound > 30m^2	0.706	0.001
mound < 10 m^2 vs. mound 10- 30m^2	0.514	0.001
mound < 10 m^2 vs. mound > 30m^2	0.658	0.001
mound 10- 30m^2 vs. mound > 30m^2	0.424	0.001

As termitarium surface area increased, indicator species representative of the matrix decreased in abundance. Three of the four species (75%) common to termitaria <10 m^2 were indicator species for matrix habitat (table 2.4). By areas of between 10 and 30 m^2, only 3 of 8 indicators (less than 40%) were of matrix origin. At surface areas > 30 m^2, only indicator species representative of mounds occurred, indicating a marked difference in edaphic conditions at this surface area, relative to the matrix.

The suite of woody plants on mounds differs taxonomically and possesses different functional traits, relative to the matrix. As much as 74 % of mound indicators bear fleshy fruit vs. 33 % for matrix; 33% represent species from riparian assemblages vs. nil for matrix; 21% are evergreen vs. nil for matrix. In this study, the principal families (as characterized by mound indicator species) where the Ebenaceae (16%) and Capparaceae (12%), while indicators from the families Anacardiaceae, Bignoniaceae, Boraginaceae, Olacaceae, Rhamnaceae, Sapotaceae, Solanaceae only occurred on mounds. The matrix was characterized by the nitrogen-fixing Fabaceae (33%; appendix 2.1).

Table 2.4. Indicator values for woody plant species in the woodland matrix and on large termitaria > 30 m^2, and the frequency of occurrence of such indicator species on termitaria < 10 m^2 and 10-30 m^2 (species listed were present in at least 20% of sites). Mounds < 10 m^2 contained predominantly matrix indicator species. Mounds of 10-30 m^2 harboured a mix of mound and matrix indicator species.

Woodland Matrix (n = 43)	Indicator Value	% occurrence Small Termitaria <10m^2 (n = 30)		% occurrence Termitaria 10-30 m^2 (n =27)		Large Termitaria >30 m^2 (n = 38)	Indicator Value
Catunaregam taylorii	48***	*B.boehmii*^{M}	57	*B.boehmii*^{M}	47	*Euclea divinorum*	87***
Boscia salicifolia	43***	*C.apiculatum*	17	*C.molle*	37	*Maerua prittwizii*	78***
Cassia abbreviata	40**	*C.collinum*	17	*D.kirkii*	33	*Capparis tomentosa*	72***
Terminalia sericia	38***	*C.molle*	13	*E.divinorum*^{T}	30	*Combretum mossambicense*	68***
Dichrostachys Cinerea	37***	*P.maprouneifola*^{M}	12	*C.mopane*^{T}	20	*Manilkara mochisia*	60***
Brachystegia boehmii	34***	*C.taylorii*^{M}	10	*C.collinum*	20	*Flueggea virosa*	56***
Pseudolachnostylis maprouneifolia	25***	*E.divinorum*^{T}	10	*C.mollis*^{T}	17	*Colophospermum mopane*	55***
Brachystegia spiciformis	24***			*A.nilotica*^{T}	17	*Diospyros quiloensis*	50***
Kirkia acuminata	23***			*C.taylori*^{M}	17	*Acacia nilotica*	50***
Julbernardia globiflora	22***			*F.indica*	13	*Lannea schweinfurthii*	47***
Crossopteryx febrifuga	21***			*C.mossambicense*^{T}	13	*Berchemia discolor*	46***
Pavetta schumanniana	21***			*P.maprouneifolia*^{M}	13	*Ximenia americana*	42***
Combretum apiculatum	17					*Feretia aeruginescens*	32***
Combretum collinum	11					*Ehretia amoena*	25***
Combretum molle	26					*Diospyros senensis*	25***
Flacourtia indica	10					*Commiphora mollis*	22***
						Markhamia zanzibarica	21***
						Solanum delagoense	20***
						Diospyros kirkii	16

Indicator values generated by PC-Ord (McCune and Mefford 1999) range from 0 to 100.

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

T denotes termitarium indicator species, *M* denotes matrix indicator species

Discussion

Through their foraging activity and distribution, *Macrotermes* termites engineer habitat heterogeneity that impacts on the spatial patterning and composition of woody plant assemblages and species. Even at very small surface areas, mound and matrix soils differed. In this study, three distinct area-related assemblages emerged, and mound-based indicator species increased with mound surface are, as matrix indicators declined. The process of establishment of the mature assemblage involves two distinct processes: the effects of termite foraging; and the effects of tree structure and demography. Mound-based species emerged as functionally (clay and nutrient-adapted vs. dystrophic-adapted, fleshy-fruited vs. pod-bearing, evergreen vs. deciduous, tall-structured vs. shorter trees), taxonomically (Capparaceae and Ebenaceae vs. Fabaceae) and geographically (harbouring species typical riparian vs. dystrophic soils) different from matrix species.

Although distinct differences arose for both soil composition and assemblages related to mound surface area, such differences probably represent a continuum from matrix conditions to those of large mound communities, with small termitaria closely resembling matrix conditions, and medium sized termitaria representing an intermediate condition between matrix and large termitaria. Although mounds are small relative to the surrounding woodland (covering less than 5% of the study area), the strong interaction between patch (the mound) and woodland matrix (through termite foraging) affects the entire miombo system. In establishing conditions for woody plant assemblages and species generally absent from, and with different functional traits to those of the matrix, *Macrotermes* termites open niches in a dystrophic woodland that can be expected to impact on both diversity and overall ecosystem function.

Findings were reached through analysis that required the reduction of the sample size of small mounds (n) from 30 for mounds < 10 m^2 and 27 for mounds 10 – 30 m^2, to 6 and 9 respectively, to ensure comparison of assemblages at equal areas. Greater sample numbers (n) could have been generated, but this would have involved repetitively incorporating mounds already randomly included in a given site, to generate new samples. Despite reduced sample size (1) the ANOSIM produced statistically significant results; (2) these samples actually represented 30 and 27 sites respectively; (3) PRIMER findings were

confirmed by PC-Ord, as a strong overlap between indicator species appearance/disappearance and the surface areas used in PRIMER emerged.

The cumulative changes in species composition in relation to termitarium size, and the addition of woody species with functional traits not characteristic of the miombo woodland matrix, is best approached by considering the potential steps in assemblage development as mounds enlarge. The theory of patch dynamics provides a structured framework from which to consider how termite (and mound-based woody plant) induced soil enrichment interacts with woody plant assemblages that in turn establish a separate soil-enriching relationship with vertebrates within the system. The process is staged: formation (seedling establishment and growth of a large tree); expansion (gradual canopy extension); patch colonization (seed dispersal); patch resource dynamics (sustained enhancement as other plants and animals occupy the shaded and fertile island beneath the canopy) and lifespan (at least as long as that of the tree; Belsky and Canham 1994). Often, this effect outlasts the initiating event, as patchy nutrient concentrations are maintained (Scholes 1990, Dean et al. 1999).

Soil organisms can affect the spatial patterning of plants (Ettema and Wardle 2002). Patches form as *Macrotermes* termites (themselves influenced by the spatial organisation of woodland litter) forage in dystrophic miombo matrix soils, elevating pH, and concentrating clay and nutrients (table 2.1). Although mounds <10 m^2 are still characterised by matrix woody indicators (75%), early changes in soil nitrogen (30% elevation) and other micronutrients allow for the establishment of tree species foreign to the matrix (for e.g., *Euclea divinorum*).

Expansion occurs as *Macrotermes* termites set up gradients of resource availability. This favours establishment and germination of a suite of woody plants more adapted not only to increasingly eutrophic soils, but also to the activities of the termites themselves (competition between plants and micro-organisms for nutrients and space can determine plant nutrient acquisition; Korsaeth et al. 2001, Ettema and Wardle 2002). Further termite activity elevates soil N, which at high levels can limit woody structure in savannas (Sankaran et al. 2008). We found that larger mounds had higher levels of soil N. At mound areas between 10 - 30 m^2, N is 8 times greater, and beyond 30 m^2, is 70 times greater than matrix

concentrations, on average. Matrix soils, characterised by nitrogen-fixing Fabaceae and ectomycorrhizal Caesalpinioideae (which together comprise 42% of matrix indicator species), Rubiaceae (25%), and Combretaceae (9%) become increasingly nitrogen-enriched and systematically lose woody species from these families. Alternatively, the matrix, which is low in P, may offer a competitive advantage to the ectomycorrhizal species, which are thought to better exploit dystrophic soils low in P (Frost 1996). As mounds enlarge, woody plant richness increases logarithmically, suggesting that ultimately the limiting effects of resources and propagules on species constrain equilibrium diversity (MacArthur and Wilson 1967). Increased surface area also improves recruitment as the probability of acquiring dispersed seeds becomes greater.

Patch colonization follows from continued termite activity. Ongoing nutrient concentration on mounds gives rise to an increasingly different environment relative to the dystrophic woodland. In this study three assemblages, correlated to surface area and soil composition, emerged. Although distinct, they probably represent stages in the development of a mature assemblage. That said, the presence of assemblages that differ to one another adds further diversity to the system. Matrix and mounds < 10 m^2 were composed generally of matrix species; mounds 10 – 30 m^2 showed an even mix of mound and matrix woody plant indicator species; and mounds > 30 m^2 had no matrix indicators. The new arrivals, not characteristic of the miombo biome, differ both in genetics and guild, and provide some clues as to the source of their propagules. Although not specifically tested for, mound indicator species seem to be functionally different to those found in the matrix, and it is possible that some form of vegetation zonation occurs on larger mounds. Mounds were characterized by fleshy fruit-bearing indicator species, often representative of riparian assemblages, and all evergreens were mound-based. The families Ebenaceae and Capparaceae were well represented in mound assemblages, whilst Anacardiaceae, Bignoniaceae, Boraginaceae, Olacaceae, Rhamnaceae, Sapotaceae, Solanaceae occurred only on mounds (appendix 2.1).

The establishment of fruiting trees is often limited by potassium [K] (Milewski 1982, Hughes et al. 1993). The matrix is deficient in K; mounds are K-rich (with concentrations > 3 times matrix levels),

which may favour the establishment of fruit-bearers like Ebenaceae, Capparaceae, Anacardiaceae, Boraginaceae, Rhamnaceae, Sapotaceae and Solanaceae. High clay content increases water retention, offering competitive advantages for certain plant species to establish (Groen et al. 2008). For southern African savannas, Jacobs et al. (2007) showed that fine-particle, nutrient-rich (secondary to frequent animal use, savanna fires depositing atmospheric nitrogen, upstream nutrient transport and deposition) savanna riparian soils sustain evergreen woody plant assemblages. Clay content doubles as mounds enlarge and this, together with differences in hydrology relative to the matrix (Turner et al. 2006), can influence seedling establishment and recruitment of evergreens, fleshy-fruited trees, and trees from riparian assemblages.

The patch resource dynamics of large termitaria involve a complex interplay between soil and plant resources, and disturbance (fire and herbivory). Termite activity establishes the patch; many factors assist in maintaining it. Increased organic matter at enriched sites leads to increased ion exchange capacity, which can enhance nutrient retention. Savanna canopy trees can themselves enrich soil, as large roots transport and concentrate nutrients (Kellman 1979, Belsky et al. 1989, Belsky and Canham 1994). Important too is the influence of leaf litter on not only soil nutrients, but on soil organisms, fire regimes, and other competing woody species (Binkley and Giardina 1998). The establishment of large trees with taller structure on mounds (Fleming and Loveridge 2003, Traoré et al. 2008, Joseph et al. 2011) creates a sub-canopy microclimate fostering the establishment of further woody species (Belsky and Canham 1994, Dean et al. 1999). The roots of these large trees can in turn add nutrients to the soil (Kellman 1979). This is followed by the occupation of the shaded and fertile island by other animals. Termitaria are hotspots for herbivores, cavity using birds, small mammal diversity, and their fruiting trees are predominantly bird dispersed (Fleming and Loveridge 2003, Loveridge and Moe 2004, Joseph et al. 2011). Defecation, urination and regurgitation add nutrients, and endozoochory brings in propagules from other biomes (e.g., the riparian environment). Once mounds establish mature assemblages, dispersal to near neighbours is likely to accelerate the process (densities of large termitaria in my study where 2 ha^{-1}). Fires too can

decrease soil nitrogen (Blair 1997), and my findings in chapter 5 demonstrate that termitaria are less affected by fire than the surrounding matrix.

Persistence is a common characteristic of nutrient patches (Belsky and Canham 1994), and patch lifespan is likely to far exceed the active and occupied phase of large termitaria. Mounds can be ancient structures, providing woody assemblages ample time to mature. Belsky and Canham (1994) noted that lifespan of a patch would at least outlast the life of a principal canopy tree. Patterns of tree-patch enrichment also suggest that even if a mound is abandoned by termites, the process of enrichment through the already extant large trees might continue (Kellman 1979). Scholes (1990) found that anthropogenically nutrient enriched areas are maintained as the enhanced productivity continues to attract browsers and grazers, and can be up to 1000 years old. The effects of termitaria may be even longer than this; Potts (2009) dated nutrient rich areas of termite origin (Moore and Picker 1991) to be in excess of 20 000 years old.

The emergence of multiple woody plant assemblages with species that differ functionally, geographically and taxonomically from the dystrophic miombo matrix directly influences woody plant species diversity. Implications for niche opportunities and woody plant functional diversity are less clear. With a growing consensus that functional diversity is important to ecosystem processes, and that species function can itself have important impacts upon community assemblage (Kraft et al. 2008), *Macrotermes* termites emerge as potential drivers of woody plant functional diversity in Africa's largest woodland.

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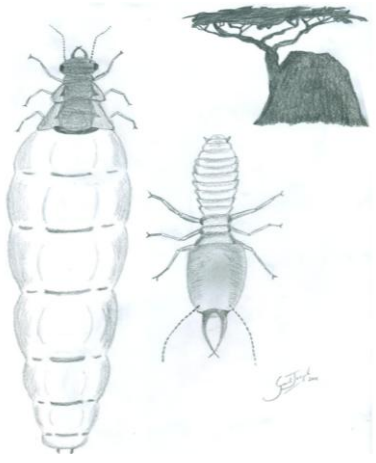


Appendices

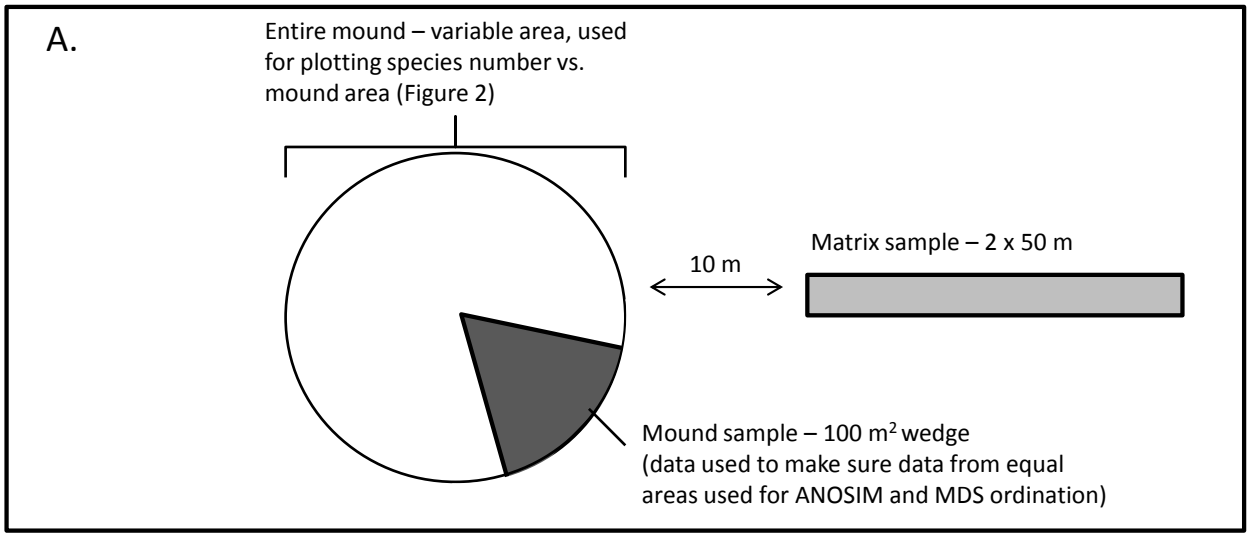
Appendix 2.1. A comparison of family, riparian origin, 'deciduousness' and fruits, for trees that characterize mounds vs. matrix. Indicator values generated by PC-Ord (McCune and Mefford 1999) range from 0 to 100, and higher values represent those most characteristic of either mound or matrix.

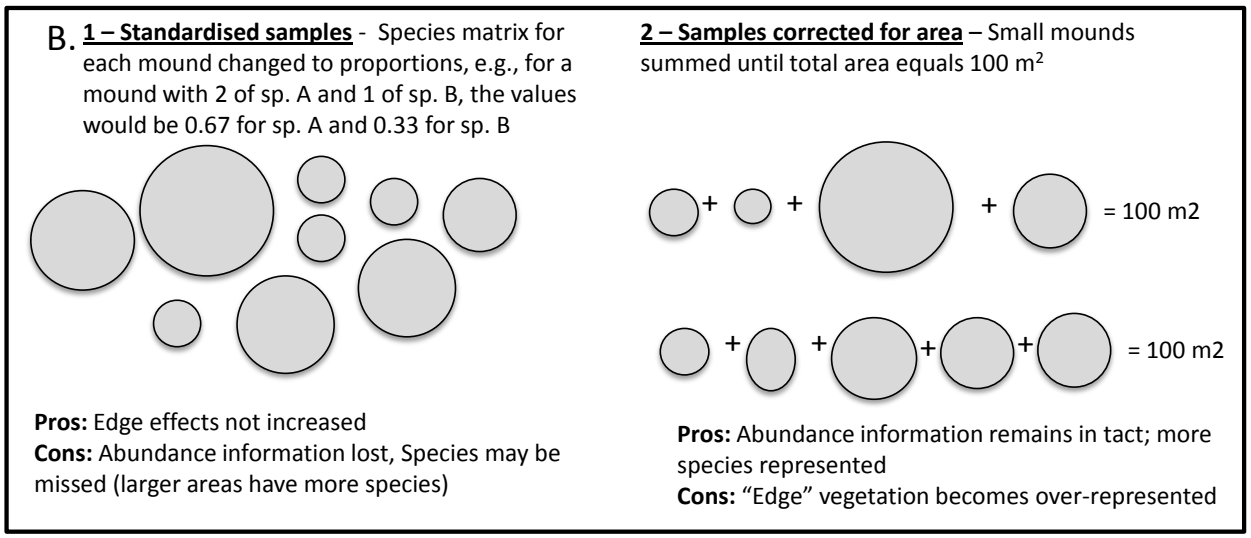
Woodland Matrix (n = 43)	Indicator Value	Family	Riparian	Evergreen/ Deciduous	Fruit
Catunaregam taylorii	48***	Rubiaceae	no	deciduous	yes
Cassia abbreviata	40**	Fabaceae-Caesalpinioideae	no	deciduous	
Terminalia sericia	38***	Combretaceae	no	deciduous	
Dichrostachys cinerea	37***	Fabaceae-Mimosoideae	no	deciduous	
Brachystegia boehmii	34***	Fabaceae-Caesalpinioideae	no	deciduous	
Pseudolachnostylis maprouneifolia	25***	Euphorbiaceae	no	deciduous	yes
Brachystegia spiciformis	24***	Fabaceae-Caesalpinioideae	no	deciduous	
Kirkia acuminata	23***	Kirkiaceae	no	deciduous	
Julbernardia globiflora	22***	Fabaceae-Caesalpinioideae	no	deciduous	
Crossopteryx febrifuga	21***	Rubiaceae	no	deciduous	yes
Pavetta schumanniana	21***	Rubiaceae	no	deciduous	yes
Combretum apiculatum	17	Combretaceae	no	deciduous	
Combretum collinum	11	Combretaceae	no	deciduous	
Combretum molle	26	Combretaceae	no	deciduous	
Flacourtia indica	10	Flacourtiaceae	no	deciduous	yes

Large Termitaria >30 m^2 (n = 38)	Indicator Value	Family	Riparian	Evergreen/ Deciduous	Fruit
Euclea divinorum	87***	Ebenaceae	yes	evergreen	yes
Maerua prittwizii	78***	Capparaceae		deciduous	yes
Capparis tomentosa	72***	Capparaceae		evergreen	yes
Combretum mossambicense	68***	Combretaceae	yes	deciduous	
Manilkara mochisia	60***	Sapotaceae		deciduous	yes
Flueggea virosa	56***	Euphorbiaceae	yes	deciduous	yes
Colophospermum mopane	55***	Fabaceae-Caesalpinioideae		deciduous	
Diospyros quiloensis	50***	Ebenaceae		deciduous	yes
Acacia nilotica	50***	Fabaceae-Mimosoideae		deciduous	
Lannea schweinfurthii	47***	Anacardiaceae	yes	deciduous	yes
Berchemia discolor	46***	Rhamnaceae	yes	deciduous	yes
Ximenia americana	42***	Olacaceae		evergreen	
Feretia aeruginescens	32***	Rubiaceae		deciduous	yes
Ehretia amoena	25***	Boraginaceae		deciduous	yes
Diospyros sinensis	25***	Ebenaceae	yes	deciduous	yes
Commiphora mollis	22***	Burseraceae		deciduous	yes
Markhamia zanzibarica	21***	Bignoniaceae		deciduous	
Solanum delagoense	20***	Solanaceae		evergreen	yes
Diospyros kirkii	16	Ebenaceae		deciduous	yes

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Appendix 2.2. Diagram to illustrate vegetation sampling in the field: only data from a wedge section of large mounds, up to 100 m2, were used for ANOSIM, MDS ordination and cluster analysis. Data for the entire mound were used to ascertain how number of species changed with total mound area. Matrix vegetation was sampled in a rectangle, to try to capture variation in vegetation at various distances from mounds **B.** Illustration of the two methods used to account for different areas of mounds < 100 m^2 in area (the smallest mound was 0.36m^2). In the first method, data were standardised, in the second method (samples corrected for area), smaller mounds were randomly selected from the small mounds dataset until their total area totaled 100 m^2.





3

Termites enhance woody plant functional diversity in a dystrophic African savanna

Abstract:

In miombo woodlands *Macrotermes* termite mounds influence woody plant species diversity by supporting assemblages of woody plants distinct from the surrounding matrix. Despite a growing consensus regarding the importance of functional diversity to ecosystem processes, the impact of termitaria on woody plant functional diversity remains poorly understood. My study sites in a heavily elephant-impacted savanna woodland in Zimbabwe were characterized by such termitaria. Termites are known to affect soil nutrients, hydrology and drainage, and elephant in high densities can affect both woody structure and fire regimes. To address whether termite mounds altered the distribution of functional traits, and increased functional diversity of woody plant communities within the ecosystem, I selected appropriate functional traits. These related specifically to soil resources (eg. water and nutrients), and disturbance (e.g., fire, elephant herbivory). I compared relative representation (i.e. abundance) of response functional groups between mound and matrix habitats, and asked whether presence of mounds increased functional diversity within the system. Although species representing most functional groups were found within both mound and matrix habitats, the relative abundance of species from the various functional groups differed between mound and matrix for both types of functional group classification (soil resources / disturbance). Traits associated with termitaria included greater tree height, leaf nitrogen and phosphorus, and palatability. The matrix favoured tree species with ectomycorrhizae in their roots. Many groups were characterized by species belonging to the same family, suggesting that environmental filtering has acted on phylogenetically-conserved traits. Even with species richness accounted for, 'matrix plus mound' plots were significantly more functionally diverse than matrix plots alone, for both measures of response functional diversity. Communities that contain species with a variety of responses to disturbance are usually better buffered against environmental perturbation. That the relative abundance of species from the response functional groups differed between mound and matrix habitat suggests that the system is better equipped to handle disturbances. The study system and results provide an example of the far-reaching effect of a soil organism in driving functional diversity in above-ground woody plant communities through provision of fine-scale spatial heterogeneity.

Introduction

Our understanding of the relationships between biodiversity and ecosystem function is complicated by spatial heterogeneity. Spatial heterogeneity can play a stabilizing role in ecosystems via such mechanisms as reducing the net frequencies of interspecific interactions (e.g., competition and predation; Pascual et al. 2001), providing spatial subsidies (Polis et al. 1997), and rescue effects (Holyoak 2000). The importance of biodiversity for ecosystem processes is determined by the functional traits of individual species and their interactions, rather than by species number *per se* (Tilman et al. 1997, Díaz and Cabido 2001, Loreau et al. 2001). The functional traits of organisms influence the biotic and abiotic environment, and through co-evolution and adaptation, these factors in turn influence the functional traits found within ecological communities (Chapin et al. 2000, Díaz and Cabido 2001). It is well known that fine-scale spatial heterogeneity can influence biodiversity (Pickett and Cadenasso 1995, Beckage and Clark 2003), yet relatively few studies have addressed effects on functional diversity. In this paper, I explore whether the spatial heterogeneity created and maintained by the foraging activities of a soil organism (*Macrotermes* termites) can drive functional diversity in aboveground woody plant communities. Although the heterogeneity provided by termitaria occurs at the fine scale (influencing alpha diversity) relative to the entire study ecosystem (accounting for less than 5% of total woodland area), it covers large areas (> 1000 km^2) at densities of 2 mounds ha^{-1} (Joseph et al. 2011), and can be expected to have effects on ecosystem functioning at larger scales.

My study site in Chizarira National Park (CNP), central western Zimbabwe, contained large termitaria (Macrotermitinae: *Macrotermes*). *Macrotermes* (Isoptera) foraging creates soils rich in clay, nutrients (notably nitrogen and phosphorus) and bases (Watson 1977, Malaisse 1978, Button et al. 1983, Frost 1996) relative to the surrounding dystrophic miombo woodland soils (Huntley 1982). Termitaria support distinct assemblages of woody plants (Fleming and Loveridge 2003, Bloesch 2008, Moe et al. 2009, Sileshi et al. 2010). These are characterised by fruiting and evergreen species (Fleming and Loveridge 2003, Joseph et al. 2011), usually from eutrophic habitats beyond the miombo system (e.g., riparian, rocky or eutrophic lowveld habitats, Cole 1982, Huntley 1982, Coates Palgrave 2005). Woody plants on

termitaria are thought to be less fire-exposed and more fire sensitive (Sileshi et al. 2010) and are important forage sources, being preferentially browsed by large ungulates because of the higher nutrient content of their leaves (Holdo and McDowell 2004, Loveridge and Moe 2004). In East Africa, Pringle et al. (2010) demonstrated that termitaria increased primary, secondary and tertiary productivity for the entire system, and concluded that spatial pattern generated by termitaria increases overall ecosystem productivity. The Zimbabwean miombo system has parallels in large, elevated, vegetated mounds (fig. 3.1) that offer important habitats to small mammals, cavity-using birds, and unique woody species (Fleming and Loveridge 2003, Joseph et al. 2011).

Figure 3.1. *Macrotermes* mounds within Chizarira National Park harbour tall trees that are often not represented in the surrounding matrix.

CNP is currently in a state of change, because of both herbivory (notably elephant browsing) and fire. Elephant at high densities open up woodland canopies, allowing an increase in grass cover that supports intense fires, converting woodland to grassland (Bond and van Wilgen 1996, Mapaure and Campbell

2002). Within CNP, thirty years of exposure to high elephant densities has converted the previously tall Caesalpinioideae woodland to structurally shorter shrub and grassland (Thomson 1974), with tall trees mostly confined to termitaria (Joseph et al. 2011).

Functional diversity is defined as "the value and range of those species and organismal traits that influence ecosystem functioning" (Tilman 2001, pg. 109). Consequently, studies about functional diversity are concerned with measuring functional traits, those aspects of organisms' phenotypes that influence ecosystem processes (Petchey and Gaston 2006). Species can be classified functionally using traits that are important in, for example, their responses to environmental factors, or their effects on ecosystems, giving rise to the concepts of 'functional response' and 'functional effect' types. This study involves the influence of soil nutrient resources and the disturbances of elephant herbivory and fire on woody plants (Mapaure and Campbell 2002), and questions have been addressed from the perspective of functional response groups. Plants that group together because of functional response are those that respond similarly to the abiotic and biotic environment (e.g., resource availability and disturbance). Functional effect types on the other hand group together by virtue of having similar effects on ecosystem process (for example trophic transfer and primary productivity) (Díaz and Cabido 2001). Therefore, having a diversity of responses within a system (i.e., high response diversity) can protect against loss of ecosystem function when ecosystems undergo disturbance (Elmqvist et al. 2003, Folke et al. 2004).

Woody cover in savannas is influenced by (1) rainfall, (2) fire, (3) herbivory, and (4) soil nutrients (Sankaran et al. 2005). Given the nutrient-concentrating effects of termitaria on miombo soils, and frequent seasonal fires in the presence of high elephant densities, I focused on functional groupings based on (1) woody plant responses to soil resources, and (2) responses to disturbance, using traits outlined in Cornelissen et al. (2003). From these two perspectives of functional response, I asked:

1) Does representation of woody plant functional groups differ between mound and matrix?
2) Does the presence of termitaria add functional diversity to the system?

Methods

Study area

This study was carried out in the miombo woodlands of CNP in north-western Zimbabwe, with field visits in November -December 2007, April - May 2009 and November - December 2009. The wet season is usually from November to April, followed by a cool dry season from May to July and a hot dry season from August to November. Mean annual temperature across the park is 20 - 22.5°C (maxima: October 32.5-35°C, July 22.5-25°C; Torrance 1965). Mean annual rainfall is 600mm-800mm (annual coefficient of variation of 25-30%; Lineham 1965).

Field Methods

Vegetation data were collected from 36 paired mound-matrix plots. Only large termite mounds (> 2 m tall or > 10m wide) were surveyed. I estimated mound surface area by modelling mounds as cone-shaped, and sampled 100m^2 of mound (selected by randomly choosing a compass bearing connecting the centre of the mound to its perimeter, and using this radius as the southernmost aspect of a pie-shape). Each 100 m^2 of mound was compared to an adjacent matrix plot also measuring 100 m^2 (50 m by 2 m), a shape chosen to ensure a representative sampling of the woodland matrix, because herbivore activity is often greater closer to mounds. Matrix plots were set along randomly chosen compass bearings radiating out from the mound, starting 10 m from the mound perimeter. For each mound-matrix plot, all woody plant species and their heights and number of stems were recorded.

Trait selection and measurement

I included species that occurred on at least 80% of mound and 80% of matrix plots and together represented 90% of aboveground biomass (Cornelissen et al. 2003), based on plant height and using the formula employed by Higgins et al. (2007) to estimate biomass. This yielded 36 species (listed in appendix 3.1), 15 of which were predominantly on mounds vs. 18 that were predominantly on matrix plots, with three species common to both. I followed standardised protocols outlined by Cornelissen et al. (2003) for collecting and measuring functional trait data.

There is reliable evidence for linking measurable functional and morphological traits to edaphic conditions and disturbance regimes (Augustine and McNaughton 1998, Chapin 2003, Mason et al. 2010). Functional groupings depend on trait selection, because plants that function similarly share a set of key functional traits relative to the function of interest (Grime and Hunt 1975, Lavorel and Garnier 2002). Cornelissen et al (2003. pg. 338) catalogue the association of functional traits with plant responses to (amongst other things): (1) soil resources, (e.g., nutrients and moisture); and (2) disturbance, (i.e., any disturbance that may destroy plant biomass, such as herbivory, fire, or extremes of climate). The traits that I used and the predictive information they yield are given in table 3.1, based on guidelines by Cornelissen et al. (2003), Díaz et al. (1999), Lavorel and Garnier (2002), and Richardson-Kageler (2004). For measurements used, see appendix 3.2. Regarding nutrient uptake strategy, due to restricted knowledge, the fact that few species in miombo woodland have vesicular-arbuscular mycorrhizae, and the anomalies that exist for individual species (for example, *Pterocarpus* species can be ectomycorrhizal in Zambia (Högberg 1986), but nodulated and endomycorrhizal in Tanzania (Högberg 1982), I have simplified the trait to reflect three groups: those that fix nitrogen (by any mechanism), those that do not, and those with ectomycorrhizae.

Data analysis

To ensure that the biological variation within each trait was treated equally, I standardised the trait data so that each trait had a mean of zero and a standard deviation of one (Petchey and Gaston 2006). I then weighted some traits. For example, seed morphology is a single trait. However, I used sphericity, length and breadth to represent this trait (i.e., 3 variables), and thus gave each variable a 1/3 weighting to prevent bias towards seed size and shape (Laliberté and Legendre 2010).

Table 3.1. Woody plant functional traits reflecting response to soil resources (eg. water and nutrients) and disturbance (e.g., fire, elephant herbivory). The asterisk denotes traits included for evaluation.

Woody plant trait ca = categorical c = continuous, o = ordinal, n = nominal	**Comments on predictive information offered by each trait**	**Response to soil resources**	**Response to disturbance**
Whole-plant traits			
Growth form (ca)	Adaption to herbivory	*	*
Life form (ca)	Survival likelihood	*	*
Plant height (c)	1) Fire and disturbance survival 2) Correlates with rooting depth	*	*
Leaf traits			
Specific leaf area (c)	1) Potential relative growth rate 2) Mass-based photosynthetic rate 3) Lower if resource-stressed biotope	*	
Leaf size (c)	1) Leaf energy & water balance 2) Influenced by nutrients & disturbance	*	
Leaf N:P ratio (c)	1) N correlates to maximum photosynthetic rate 2) Nutritional quality is associated with N or P 3) Ratio (N:P) determines whether N or P is is more limiting	*	*
Leaf lifespan (o)	Corresponds with strength, and defence against herbivory		*
Leaf phenology (o)	Evergreens invest more in leaf protection	*	*
Leaf palatability (o)	Vertebrates , as per Walker (1980) Correlates to nutritional quality, chemical defence		*
Stem & below ground traits			
Bark thickness (o)	Defence from fire, herbivores, pathogens	*	*
95% Rooting depth (c)	Belowground competition for water / nutrients	*	*
Nutrient uptake strategy (ca)	Reflects adaptation to nutrient availability	*	*
Regenerative traits			
Dispersal mode (ca)	Propagation potential (distance and number)		*
Dispersal shape & size (c)	Increased sphericity correlates with longevity		*
Seed mass (c)	1) Smaller, disperse further, in greater numbers 2) Larger seeds use added resources to assist seedling establishment and survival	*	*
Resprouting capacity (o)	Measure of persistence following disturbance	*	*

I calculated functional diversity (FD) by using functional richness as the diversity index, and identified functional groups by converting the species by trait matrix into a distance matrix using Gower distance because it allows individual traits to be weighted differently (Podani 1999), and allows use of quantitative and qualitative traits together (Podani and Schmera 2006). I then clustered the matrix using the 'average' method in the FD package in R (Laliberté and Shipley 2010), which was chosen after checking for the highest cophenetic correlation (0.89 for response to soil resources, 0.69 for response to disturbance). Each species was therefore given a measure of similarity with every other species, based on the functional traits used.

Comparing whether woody plant functional groups differed between mound and matrix

I placed species into functional groups using the FD package in R. To explore the functional relationships of woody plant species, I specified (*a priori*) six functional groups for both response to soil resources and response to disturbance. Although FGR (functional group richness) ignores functional differences occurring between species in the same group, and the level of difference between groups can be arbitrary (Petchey and Gaston 2006), the groups it identifies can be used to give an overall picture of whether, and how, functional groups might differ between termitarium and woodland habitat. To do this, I conducted goodness of fit tests to ascertain if there was any difference in relative representation of functional groups between mound and matrix plots, using square root abundance data. I square-root transformed the data to minimise the effects of small but very common species. In situations where there were significant differences between matrix and termitaria plants, I carried out a SIMPER analysis in PRIMER (Clarke and Gorley 2001) to explore the traits that accounted for the observed differences between species from the two habitats.

Comparing functional diversity

The FD of each plant assemblage was measured as the total length of branches needed to connect all of the species in the assemblage (Petchey and Gaston 2006). To determine whether matrix plus mound plots were more functionally diverse than matrix plots alone, species richness had to be accounted for. Each time a species

is added to an assemblage, the FD can increase. It would be invalid to compare, for example, the functional diversity of a matrix plot with *n* species to the functional diversity of that matrix plot plus its mound plot (with *k* species), which would then have *n* + *k* species. I thus compared the FD value for the observed assemblages of *n* species against 999 random assemblages of *n* species from the full set of species used in the analysis, using a null-model where I shifted taxa labels across the dendrogram. This gave each plot a ranking out of 1000, with higher numbers indicating higher functional diversity. I compared the rankings out of 1000 for each matrix plot with its paired termitarium plus matrix plot (e.g., matrix plot 1 *vs.* matrix plot 1 plus termitarium plot 1), using a pairwise Wilcoxon test for matched pairs. All analyses were conducted in R (R Development Core Team 2010). So, for each pair of plots (matrix with n species plus termitaria with k species) two null models were run: one with n species and one with n+k species. For these models all species present in the study ("full set of species") were allowed to be selected to form random communities. Then, each of the field situations – matrix, and matrix plus termitaria – were ranked according to the random FD distribution with, respectively, *n* and *n+k* species. In this way I could compare the observed FD of each situation with that expected by chance (controlling for number of species), and in so doing, to draw a comparison of whether the situation 'matrix plus termitaria' was more functionally diverse than matrix alone.

Results

Of the woody plants surveyed, 36 species, represented by 5332 individual plants, met the requirements of being present on at least 80% of plots (Cornelissen et al. 2003).

1. Differences in woody plant functional groups, mound vs. matrix

Response to soil resources

The dendrograms in fig. 3.2 show the functional relationships between the 36 species in my plots in CNP, reflecting their responses to soil resources and to disturbance.

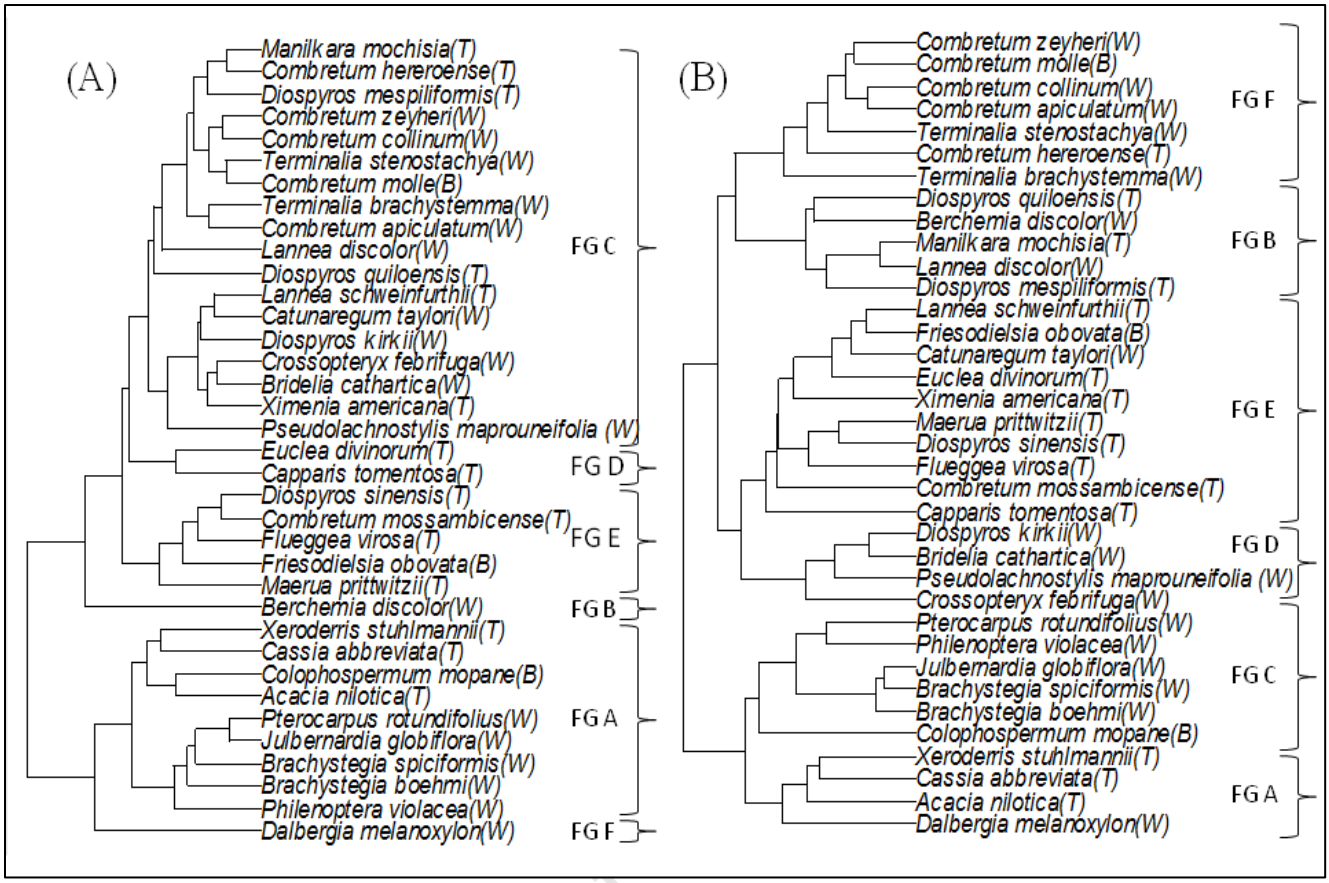


Figure 3.2. Functional relationships between the dominant woody plant species in CNP, based on (A) response to soil resources and (B) response to disturbance. (*T*) represents plants found primarily on termitaria, (*W*) represents those found primarily in the woodland matrix, and (*B*) those that tend to be found on both *(T)* and (*W)* plots. Functional groups are denoted by the letters A to F.

Species with shorter connections between them are more functionally similar. For example, *Combretum zeyheri* and *C. collinum* respond in a similar way to soil conditions, but *Pseudolachnostylis maprouneifolia* and *Phileneptera violacea* respond quite differently. Although there was some overlap between termitarium and woodland habitat when six functional groups were selected, it is evident from the dendrogram that division into smaller groups gives separate clusters for mound and matrix. Regarding response to soil resources, for example, functional group A (a mix of woodland and matrix species) is at

finer resolution composed of two subgroups that reflect distinct mound and matrix affiliations. When relative representation (i.e., abundance) of functional groups within the two habitats (woodland *vs.* termitarium) was compared, the difference was significant ($p < 0.001$, table 3.2).

Table 3. 2. Representation of functional groups on termitaria and woodland plots, based on square root abundance data. The functional groups to which each species is allocated are reported in fig. 3.2 and appendix 3.1.

Response to soil resources					
Functional group	***Woodland***	***Termitarium***	χ^2	***d.o.f.***	***p***
FG A	208	103	315.85	5	<0.0001
FG B	0	17			
FG C	360	118			
FG D	1	89			
FG E	18	320			
FG F	36	15			
Response to disturbance					
Functional group	***Woodland***	***Termitarium***	χ^2	***d.o.f.***	***p***
FG A	55	39	288.97	5	<0.0001
FG B	13	74			
FG C	186	76			
FG D	50	0			
FG E	184	430			
FG F	124	35			

For response to soils, SIMPER analysis identified six traits responsible for 75% of the observed difference (table 3.3), although none of the traits could be considered good discriminators across all sites (i.e., the square distance/standard deviation ratio was low). Nutrient uptake strategy accounted for 30.24% of the difference explained. Ability to resprout (10.55%) and months/year without leaves (9.4%) were both lower for plants on mounds. Leaf N (9.03%) and leaf P (8.62%) were higher on mounds, whilst leaf size (8.59%) was higher for the matrix.

Table 3.3. Primary traits responsible for differences between termitarium and matrix plants for the SIMPER analyses. Note that "average values" reported are standardized values, to ensure variation within each trait is treated equally (Petchey and Gaston 2006). Actual values are bracketed with standard deviations alongside (n = nominal, o = ordinal). Species with a high dissimilarity/SD ratio contribute consistently across replicates. Therefore species with higher ratios represent better discriminating species (Clarke and Warwick 1994).

RESPONSE TO SOIL RESOURCES						
	Termitaria	**Matrix**				
Variable	Average Value	Average Value	Average Square Distance	Square Dist/ SD ratio	Percent added to difference	Cumulative percentage
Nutrient uptake strategy (*n*)	-0.34	0.25	7.75	0.81	30.24	30.24
Resprouting capacity (*o*)	-0.62 (0.6 ± 0.4)	0.54 (1.7 ± 1.0)	2.70	0.97	10.55	40.78
Months / year without leaves	-0.49 (2.1 ± 1.1)	0.32 (3.1 ± 0.6)	2.41	0.64	9.40	50.18
Leaf N (part per hundred)	0.39 (2.9 ± 1.1)	-0.27 (2.2 ± 0.7)	2.32	0.65	9.03	59.21
Leaf P (part per hundred)	0.19 (0.17 ± 0.08)	-0.29 (0.15 ± 0.03)	2.21	0.58	8.62	67.84
Leaf size (mm^2)	-0.31 (80.5 ± 120.2)	0.28 (200.1 ± 200)	2.20	0.62	8.59	76.42
Seed mass (g)	-0.224 (0.10 ± 0.10)	0.25 (0.34 ± 0.62)	2.05	0.28	7.99	84.41
SLA (mm^2mg^{-1})	0.194 (3.4 ± 1.4)	-0.19 (2.6 ± 0.71)	2.00	0.65	7.81	92.22
RESPONSE TO DISTURBANCE						
	Termitaria	**Matrix**				
Variable	Average Value	Average Value	Average Square Distance	Square Dist/ SD ratio	Percent added to difference	Cumulative percentage
Resprouting capacity	-0.623	0.544	2.7	0.97	11.85	11.85
Density of trees >6m (ha^{-1})	0.358(6.9 ± 9.8)	-0.297 (1.2 ± 0.5)	2.38	0.49	10.42	22.27
Leaf N	0.368	-0.27	2.32	0.65	10.15	32.42
Leaf P	0.186	-0.291	2.21	0.58	9.69	42.11
Growth form (*n*)	-0.279	0.199	2.14	0.77	9.39	51.50
Attainable tree height (m)	-0.327 (9.4 ± 4.53)	0.216 (10.4 ± 4.3)	1.99	0.72	8.74	60.24
Nutrient uptake strategy	-0.171	0.122	1.94	0.81	8.49	68.73
Palatability (Walker 1980, *o*)	0.143	-0.329	1.88	0.71	8.26	76.99
Seed mass	-0.149	0.164	0.911	0.28	3.99	80.98
Dispersal mode: indehiscent(*n*)	0.255	-0.15	0.909	1.00	3.98	84.96
Dispersal mode: endozoochory	0.147	-0.147	0.907	1.04	3.98	88.94
Seed shape & size (sphericity)	7.66E-2	3.45E-2	0.878	0.71	3.85	92.78

Response to disturbance

The dendrogram for functional groups based on response to disturbance did not show clear separation between termitaria and matrix woody plant species at low resolution, although within the larger groups there was some separation between mound and matrix species (fig. 3.2B). Species also tended to group according to family. For example, the group that includes *Pterocarpus rotundifolius* to *Dalbergia*

melanoxylon are all members of the Fabaceae, and the group from *C. zeyheri* to *Terminalia brachystemma* are all Combretaceae. Again, when relative abundances are considered, the differences in representation between the functional groups are significantly different ($p < 0.001$, table 3.2).

Eight different traits explained 75% of the observed differences in response of woody species on disturbance (table 3.3). These were resprouting response after fire (lower on termitaria; 11.9%), number of trees > 6 m, leaf nitrogen, and leaf phosphorus (all higher on termitaria, and each explaining approximately 10% of difference observed), growth form (more trees in the matrix; 9.4%), maximum attainable height (higher in matrix, 8.8%), nutrient uptake strategy (ectmycorrhizal tree species in matrix; 8.49%) and palatability (higher on termitaria, 8.5%).

2. Mound influence on functional diversity

Functional diversity rankings were significantly higher for mound and matrix plots together than for matrix alone in terms of (1) response to soil resources (*matrix & mound*: median = 713.5; $Q_1 = 610.5$; $Q_3 = 902$; *matrix*: median = 280.5; $Q_1 = 144.5$; $Q_3 = 536.8$, $p < 0.001$), and (2) response to disturbance (*matrix & mound:* median = 798, $Q_1 = 467.0$; $Q_3 = 901.5$; *matrix:* median = 556; $Q_1 = 249$; $Q_3 = 695$, $p = 0.0011$).

Discussion

I found clear support for the hypothesis that fine-scale environmental heterogeneity can enhance functional diversity. The representation of functional groups was significantly different between mound and matrix habitats and, for the two aspects of functional diversity investigated, functional diversity rankings were significantly higher for mound and matrix plots together than for matrix alone. In contributing to local woody plant functional diversity, termitaria are likely to influence ecosystem function at larger scales, given their broad distribution through much of the region's southern miombo woodlands.

Many species changed membership of functional group according to the type of functional response (i.e. soil resources / disturbance) being investigated (appendix 3.1), illustrating the consequence of the different paradigms used to look at species. This variability in FD (as an anticipated consequence of the different traits used) highlights the need for appropriate trait selection and standardization depending on the functional diversity in question (Cornelissen et al. 2003). In response to soil resources, nutrient uptake strategy was the main driver of differences between mound and matrix species (explaining almost one third of observed difference), reflecting different adaptation to nutrient availability between the microhabitats. Nitrogen-fixing species were evenly distributed between mound and matrix, whereas the characteristic miombo subfamily, Caesalpinioideae, which are ectomycorrhizal species, dominated the nutrient-poor matrix. It is thought that ectomycorrhizae may contribute to uptake of phosphorous (P), in P-depleted soils (Frost 1996), and other tropical ecosystems dominated by ectomycorrhizal species have been shown to have dystrophic soils (Högberg 1982). Enriched mound soils are a consequence of *Macrotermes* foraging, and patches of raised soil fertility can have marked ecological impacts in low nutrient systems (Scholes 1990, Mobæk et al. 2005). Other traits accounting for the remaining 60% of differences observed were almost equally important (see table 3.3). Trees on mounds held their leaves for longer, allowing protracted photosynthesis, and potential early growth before seasonally-leafed species begin competing for light (Aerts 1995); Leaf N and P were higher (as expected for resource-rich environments), as was specific leaf area (SLA). SLA is generally lower in resource-stressed environments, reflecting the dystrophic matrix soils. Seed size, larger for matrix trees, emerged as an important explanatory trait; the association of species with smaller seeds (which disperse over greater area, in greater numbers), supports the observation that mound species are often derived from propagules from a distant source. Larger matrix-associated seeds probably represent an adaption to lower nutrient soils, because large seeds imply greater investment in establishment and survival (Cornelissen et al. 2003).

In response to disturbance, the ability to resprout explained the greatest observed difference (12%) between mound and matrix woody plant species. Resprouting can be a fire-adapted response in miombo

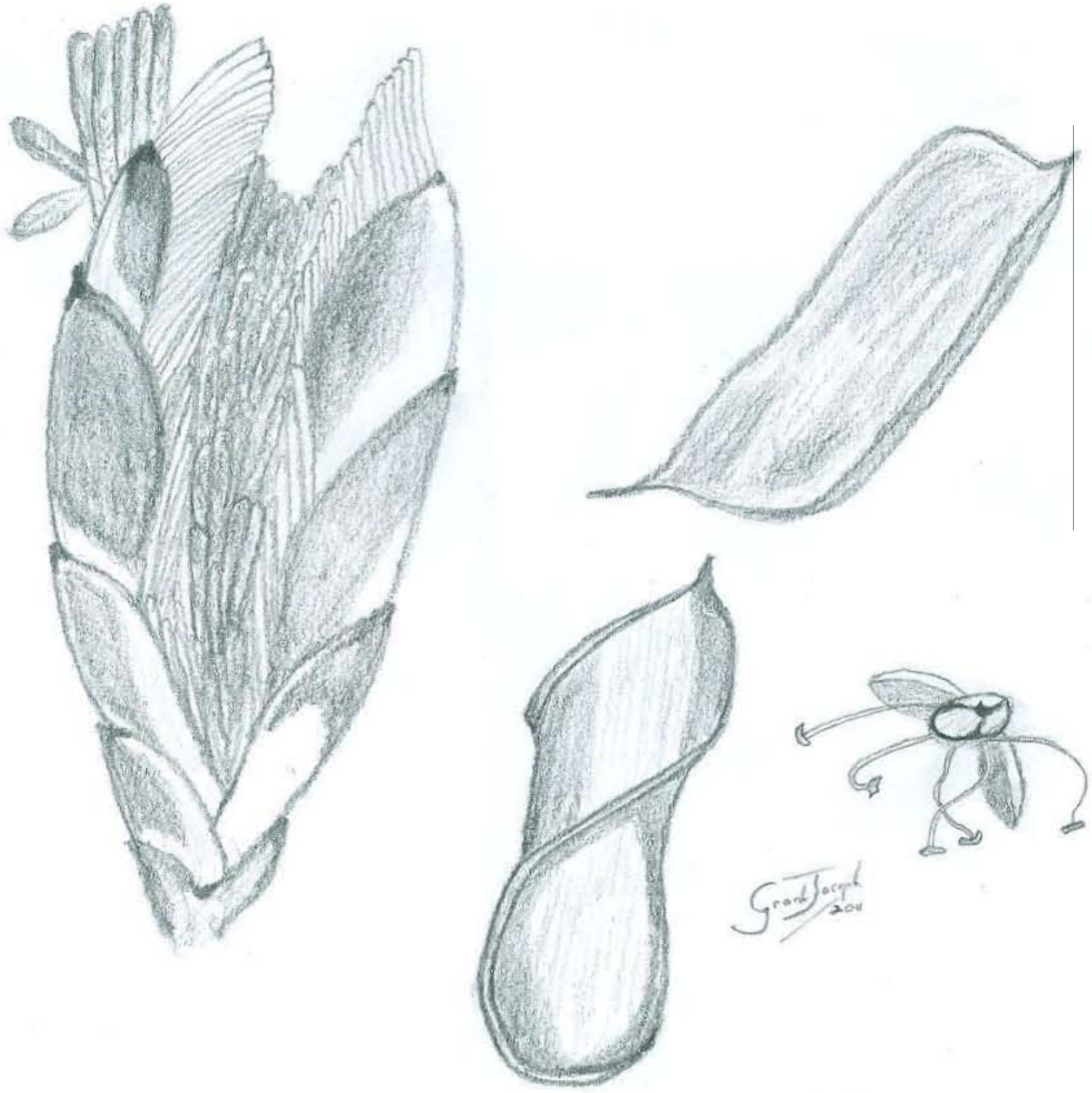
woodlands (Nefabas and Gambiza 2007), reflecting greater fire exposure for matrix than mound species (see Chapter 5). That number of trees > 6 m was higher for mounds, whereas maximum attainable tree height of a given species (i.e. 'potential height'; Coates Palgrave 2005) was higher for the matrix, reflects not only dystrophic soils, but also the documented conversion of previously tall woodland matrix trees to stumps and converted trees following elephant foraging (and the consequent intense fires; Joseph et al. 2011). Lower palatability observed for matrix plants probably reflects a response of leaves to low nutrients, more than an adaptation to disturbance.

Phylogenetically conserved traits emerged as important factors in explaining underlying community composition: species often grouped together functionally by family, e.g. members of the Fabaceae (*Pterocarpus rotundifolius, Philenoptera violacea, Julbernardia globiflora, Brachystegia spiciformis, B. boehmii, Colophospermum mopane, Xeroderris stuhlmannii, Cassia abbreviata, Acacia nilotica, Dalbergia melanoxylon*); Combretaceae (*Combretum* and *Terminalia* species) and, to a lesser extent, Ebenaceae (e.g., *Diospyros kirkii, D. mespiliformis* and *D. quiloensis*). Webb et al. (2002) suggested that phylogenetic clustering indicates environmental filtering acting on shared physiological traits, and here, the relative importance of environmental filtering and competition on plant assemblage composition and the expression of traits will require further investigation.

The importance of termitaria as sources of browse, habitat and species diversity has already been established (Konaté et al. 1999, Fleming and Loveridge 2003, Holdo and McDowell 2004, Loveridge and Moe 2004, Mobæk et al. 2005, Traoré et al. 2008, Joseph et al. 2011). This study adds functional diversity to the list, and specifically provides an example of how spatial heterogeneity created at small scales by the foraging activity of *Macrotermes* termites increases functional response diversity within a dystrophic miombo system.

Although not measured directly, there is and expectation that overlap of function [functional redundancy, 'the degree to which organisms have evolved to do similar things' (Rosenfeld 2002)] might contribute to increased resilience (the ability of a given ecosystem to adapt to change through maintenance of function; Elmqvist et al. 2003). This can be expected to contribute to resilience of the

system as a whole, as species that display a variety of responses to disturbance are often better buffered against environmental perturbation (Chapin 2003).



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Appendix 3.1. Functional group to which each species was allocated, for the different aspects of functional diversity studied. I specified that species must be placed into six groups for each type of response, these groups are denoted by the letters A to F.

Species occupying 80 % of sites, and comprising 90 % of biomass. *m* denotes matrix; *t*, termitarium; and *b*,'both'	***Soil nutrient response***	***Response to disturbance***
Acacia nilotica[t]	A	A
Berchemia discolor[t]	B	B
Brachystegia boehmii[m]	A	C
Brachystegia spiciformis[m]	A	C
Bridelia cathartica[m]	C	D
Capparis tomentosa[t]	D	E
Cassia abbreviata[t]	A	A
Catunaregam taylori[m]	C	E
Colophospermum mopane[b]	A	C
Combretum apiculatum[m]	C	F
Combretum collinum[m]	C	F
Combretum hereroense[t]	C	F
Combretum molle[b]	C	F
Combretum mossambicense[t]	E	E
Combretum zeyheri[m]	C	F
Crossopteryx febrifuga[m]	C	D
Dalbergia melanoxylon[m]	F	A
Diospyros kirkii[m]	C	D
Diospyros mespiliformis[t]	C	B
Diospyros quiloensis[t]	C	B
Diospyros sinensis[t]	E	E
Euclea divinorum[t]	D	E
Flueggea virosa[t]	E	E
Friesodielsia obovata[m]	E	E
Julbernardia globiflora[m]	A	C
Lannea discolor[m]	C	B
Lannea schweinfurthii[t]	C	E
Maerua prittwitzii[t]	E	E
Manilkara mochisia[t]	C	B
Philenoptera violacea[m]	A	C
Pseudolachnostylis maprouneifolia[m]	C	D
Pterocarpus rotundifolius[m]	A	C
Terminalia brachystemma[m]	C	F
Terminalia stenostachya[m]	C	F
Xeroderris stuhlmannii[b]	A	A
Ximenia americana[t]	C	E

Appendix 3.2. Properties measured for individual traits, as per Cornelissen et al. (2003) and Richardson-Kageler (2004).

Woody plant trait	Data type	Sub-category	unit	Method
Growth form	categorical	shrubs/ trees/ climbers	categorical	descriptive
Life form	categorical	chamaephyte/ phanerophyte/ therophyte /	categorical	descriptive
Plant height (Potential) Plant height (in system)	continuous categorical	distance between upper boundary of photosynthetic tissues and the ground trees > 6m	m	literature (Coates Palgrave 2005) Direct measure (mean height)
Specific leaf area	continuous	one-sided area divided by oven dried mass	mm^2mg^{-1}	Leaf area meter (petiole included)
Leaf size	continuous	one-sided area	mm^2	Leaf area meter (petiole and rachis exluded)
Leaf N:P ratio	continuous	ratio derived from concentrations per unit of dry leaf mass (mg g^{-1})	ratio	petiole and rachis exluded
Leaf lifespan	ordinal	time during which leaf is alive and physiologically active (in months)	months	Periodic census of tagged leaves / literature*
Leaf phenology	ordinal	number of months per year that the leaf canopy remains green	months	direct observation
Leaf palatability	ordinal	see Walker (1980)		
Bark thickness	ordinal	direct measurement	mm	direct measure
95% Rooting depth	continuous	estimates the depth, in metres, above which 95% of root biomass of a species is located	g m^{-3}	correlation with height (Coates Palgrave 2005)
Nutrient uptake strategy	categorical	nitrogen-fixer / non-nitrogen fixer/ ectomycorrhiza	categorical	literature *
Dispersal mode	categorical	wind / endo- & ecto-zoochory / ballistichory /	categorical	direct observation/ literature*
Seed shape & size	continuous	variance of length, breadth and width	variance lies between 0 and 2, and is unitless	direct measure of sphericity; mean of 10 seeds per species
Seed mass	continuous	dried mass of seed	mg	direct measure
Resprouting capacity	ordinal	capacity to reprout post destruction of aboveground tissue post fire & herbivory	mm	direct measure** (mean of 10 per species)

*(Corby 1974, Högberg and Nylund 1981, Högberg 1982, 1986, Högberg and Piearce 1986, Frost 1996, Coates Palgrave 2005)

**resprouting response post fire; matched for height (0: no resprouting; 1: some resprout tissue (<10 cm); 2: >10 cm but <30 cm of resprouting tissue; 3: >30cm of resprouting tissue; see Chapter 5)

4

Forty years of exposure to different large herbivore communities alter miombo woody plant assemblages and functional diversity on and off termitaria

Abstract

Woody plants are a vitally important feature of most savanna habitats. Although the fundamental drivers of woody plant diversity in African savannas are relatively well-studied, some notable gaps in our understanding remain. One such gap relates to the interactions between herbivory and fine-scale spatial heterogeneity. Within a typical grassland savanna matrix, grazing by a low biomass of large mammals reduces woody cover. Above a threshold of grazer biomass, woody cover increases. Browsers and mixed feeders, by contrast, consistently reduce woody cover. These effects are, however, less clear at finer scales and in smaller patches of vegetation. *Macrotermes* termite mounds, for instance, can harbour unique woody species and enhance available woody structure, with potentially system-wide consequences. I asked how 40 years of differential exposure to herbivory (grazing vs. browsing and mixed feeding vs. exclusion) interacted with spatial heterogeneity, in the form of large *Macrotermes* termitaria, to influence fine-scale woody plant species taxonomic and functional composition. I surveyed 40 mound-matrix pairs at 3 different sites in a miombo woodland in north-central Zimbabwe. I found significant differences in woody plant assemblages (1) on mounds relative to the matrix woodland; (2) between mounds across herbivory treatments; and (3) between matrix plots with differing herbivore treatments. Representation of functional groupings based on 10 functional traits characterizing herbivore impact differed for both location (mound vs. matrix) and treatment (herbivory). Plant functional diversity also differed with location and treatment. Mounds emerged as repositories of functional richness, and functional richness declined as exposure to browsers increased. Functional divergence, contrary to expectation that it would be higher in nutrient-poor soils (and increase in the face of browsing as traits that develop as an adaptation to browsing become amplified), followed the pattern of functional richness, suggesting that in some circumstances F_{Div} becomes a partial corollary of $F_{Ric.}$ Maintenance of woody plant functional evenness despite lowered functional richness showed that communities have contracted in trait space by loss of similar functional types across treatments, implying lowered functional resilience rather than lowered functional diversity. My results suggest two differing future scenarios, contingent on management: a system that despite loss of functional richness and contraction of trait space, is well adapted to being browsed and has the potential to fill the new niches as they open up; or alternatively, a system that through loss of functional richness and thinning of trait space, becomes increasingly vulnerable to breakdown of processes and invasion by alien woody species.

Introduction

One of the central questions in our understanding and management of savanna habitats is how the woody plant community responds to changes in dominant environmental regimes. Woody plant structure and composition in mesic savannas (i.e., those with mean annual precipitation > 650mm) is strongly influenced by fire, soils, and herbivory. Of these drivers, ungulate herbivore stocking rates and fire are probably the most amenable to management (Walker et al. 1987, Higgins et al. 1999, Van Wilgen et al. 2004). Using data from 161 African savanna sites, Sankaran et al (2008) found that although grazers depressed woody cover at low biomass, woody cover increased above a certain threshold of grazer biomass. By contrast, browsers and mixed feeders consistently decreased woody cover. Ungulate herbivores can influence not only the structure but also the species composition of woody assemblages (Richardson-Kageler 2003).

Changes in species composition do not occur uniformly across different functional groups. For example, herbivores can alter the functional composition of plant communities by preferentially browsing nutrient-rich, poorly defended foliage (Augustine and McNaughton 1998, Mason et al. 2010). Alterations in the functional composition of the flora can have important consequences for ecosystem processes, as there is generally a greater association between ecosystem processes and species' functional characteristics (i.e., functional composition/traits and functional types) than with species diversity (Sankaran and McNaughton 1999).

Spatial heterogeneity influences biodiversity through (amongst others) its effects on local survival and growth rates (Beckage and Clark 2003), dispersal success (Howe and Smallwood 1982, Valiente-Banuet et al. 1991), resource availability (Ettema and Wardle 2002) and disturbance regimes (Clarke 2002). Heterogeneity can contribute to the formation of distinct woodland communities relative to the surrounding matrix. In African savannas, termitaria create patchiness within the landscape by altering topography, elevating soil nutrient and clay composition, affecting hydrology and drainage, and ultimately influencing ecosystem productivity (Fanshawe 1968, Wood and Sands 1978, Lal 1987, Jones et al. 1994, Schuurman and Dangerfield 1996, Dangerfield et al. 1998, Fleming and Loveridge 2003, Moe

et al. 2009, Pringle et al. 2010, Sileshi et al. 2010). The distinct vegetation associated with termite mounds provides important forage for herbivores in African savannas (Loveridge and Moe 2004, Brody et al. 2010, Levick et al. 2010). Mobæk et al. (2005), for example, found that six of seven ungulate species spent significantly more time foraging near mounds; and Holdo & McDowell (2004) suggest that termitaria (representing about 5% of the landscape in their study) may be the source of over 25% of elephant forage.

Pressure for suitable pasture in Zimbabwe has resulted in extensive use of miombo woodlands as a source of graze and browse for livestock (Campbell et al. 1996). My study site, in miombo woodland beside Lake Chivero (northern Zimbabwe), is characterized by the presence of numerous large *Macrotermes* termitaria. Three adjacent sites separated by 40 years of different exposure to herbivory (grazer-dominant vs. browsers and mixed feeders vs. exclusion) provided a setting for testing the interactive effects of spatial heterogeneity (nutrient-rich mounds) and herbivory (grazing and browsing) on woody plant community assemblage and functional diversity.

To date, studies evaluating the effects of termitaria on woody plants have been limited to mound vs. matrix comparisons, and those that have addressed exposure to different types of herbivory have not included termitaria. The combination of habitat heterogeneity, competition and disturbance has been shown to affect dispersal and colonization rates for woody plants, and in so doing create diversity (Weiher and Keddy 1999). Aside from the finding that ungulate herbivores of different feeding guilds and densities affected abundance of woody species with different functional traits (Richardson-Kageler 2004), however, our knowledge of the effect of herbivory on functional diversity in the setting of fine-scale patches remains scant.

Given that (1) young seedlings of palatable woody species are susceptible to browsing and trampling (Seif El Din and Obeid 1971, Cumming and Cumming 2003); (2) browsers and mixed feeders consistently decrease woody cover (Sankaran et al. 2008); (3) browsing can alter woody plant diversity (Richardson-Kageler 2004) and both species and functional composition of woody assemblages (Augustine and McNaughton 1998, Mason et al. 2010); and (4) termitaria have been shown to act as a

refuge for woody structure under conditions of high herbivory (Joseph et al. 2011), I considered how termitaria might influence alpha and beta woodland plant functional community composition under different herbivory regimes.

Since functional richness (F_{Ric}) provides information on the use of available resources by woody plants, I expected it to be higher for nutrient-rich mounds. If browsing and mixed-feeding (as opposed to grazing alone) place pressure on certain traits, then F_{Ric} might be lower for browsed plots. $F_{Div,}$ ("the degree to which abundance distribution in niche space maximises divergence in functional characters within the community"; Mason et al. 2005) relates to niche differentiation via competition for available resources, and can be expected to be higher in nutrient poor areas (as coexistence in resource-limited circumstances can require specific functional niches). The evaluation of functional evenness (F_{Eve}, which explores utilization of niche space and offers predictions regarding productivity) in combination with F_{Ric} can provide additional information regarding the spread of functional traits (Mason et al. 2005, Schleuter et al. 2010). In the context of exposure to different types of herbivore impact (browsing and mixed feeding vs. grazing), and absence of herbivory, I expected the abundance of some traits to vary.

To explore these hypotheses I proceeded in two steps. First, regarding community composition, I asked (1) How does position (mound vs. matrix), and treatment (differential exposure to herbivory) affect the taxonomic composition of woody species? Then, to address the effects of herbivory (grazing vs. browsing and mixed feeding vs. herbivore exclusion) on functional diversity, I asked (2) How do location (mound vs. matrix) and long term exposure to different patterns of herbivory affect the representation of functional traits, and FD, within assemblages?

Methods

Study Site

This study was carried out in three adjacent sites within the miombo woodlands surrounding (man-made) Lake Chivero in northern Zimbabwe (fig.4.1). Each site has a different history of exposure to herbivory. Miombo is

a broad leaved deciduous woodland dominated in this area by two Caesalpinioideae species, *Brachystegia spiciformis* and *B. glaucescens*, and characterised by vegetated termitaria constructed by *Macrotermes* (Isoptera) termites that form nutrient rich hotspots (Frost 1996) and harbour a set of tree species distinct from the surrounding dystrophic matrix (Huntley 1982, Fleming and Loveridge 2003, Fig.4).

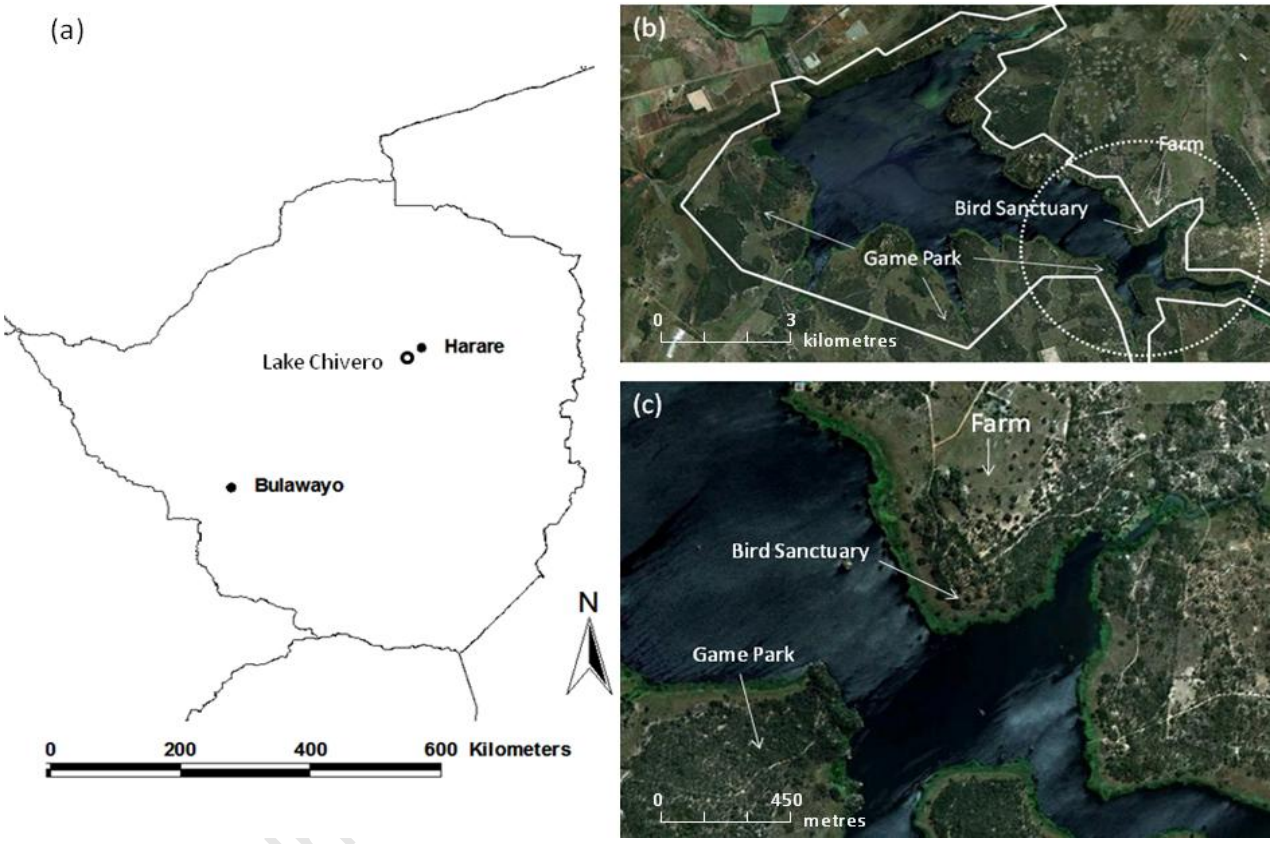

Figure 4.1(a). Schematic representation of the locality of Lake Chivero (17°52´S, 30°46´E); (b) satellite view of the entire Chivero National Park and surrounding agricultural lands; (c) higher resolution view showing study sites. (Map of Lake Chivero and surrounds, retrieved on July 4, 2011 and modified from http://www.google.co.uk/intl/en_uk/earth/index.html)

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Figure 4.2. *Macrotermes* termitaria can be massive structures (a) that support dense woody vegetation (b). Photographer: David Cumming

The 6100 ha Lake Chivero Recreational Park (LCRP) is composed of a bird sanctuary (with all large herbivores excluded) and a fenced game park of 1867 ha. The game park had expanded from 364 ha in 1959 (when it opened) to its present 1867 ha by 1970. Sampling was limited to the Ostrich Loop area of the game park, an area that had not been cultivated when the park was established. In addition to its smaller fauna, the game park contains blue wildebeest (*Connochaetes taurinus*), Burchell's zebra (*Equus burchelli*), common waterbuck (*Kobus ellipsipyrimnus*), eland (*Taurotragus oryx*), giraffe (*Giraffa cameleopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), sable antelope (*Hippotragus niger*), tsessebe (*Damaliscus lunatus*) and white rhino (*Ceratotherium simum*). Although species like waterbuck are predominantly grazers, during the dry season they also browse (Tomlinson 1979). Giraffe, eland, and kudu are browsers, and impala are mixed feeders (Skinner and Chimimba 2005). Hence, the game park is home to browsers, mixed feeders, and grazers, a combination that should be capable of limiting woody cover and influencing the composition of woody plant assemblages.

The Bird Sanctuary is separated by a fence from the 650 ha Glen Roy farm, which contains grazers in the form of Brahman cattle. In tropical dry seasons, cattle are not always able to meet their nutritional needs through dry grass (Topps 1997), and can supplement nutrition by feeding on woody shrubs. In southern Africa, some of the plant species that characterise mopane and miombo woodlands are preferred browse for cattle when grass is unavailable or of poor quality (Fritz et al. 1996). Thus, the cattle may have done some browsing during the dry season, despite being predominantly grazers. Hence this study compared three sites with at least four decades of differing land use.

The topography of the area is flat; soils at all three sites are moderately shallow and sandy, overlying granite (Munzwa 1982). All three sites are adjacent to and roughly equidistant from Lake Chivero. Two sites, the Bird Sanctuary and Glen Roy farm, are on the northern shore. Neither area has records of extensive fires. The game park is on the southern shore, and as it is close to the recreational facilities and rest camp, it too has not experienced recent or extensive fires. All sites are at similar altitude (which ranges from 1370 m to 1515 m). Site proximity ensures that all share similar rainfall and temperature. Average annual rainfall is 800 mm. Mean annual temperatures are 13 °C (mean minimum) and 25°C (maximum; Torrance 1965).

All three sites have been under the above-mentioned forms of landuse for over 40 years. The close proximity of sites was specifically chosen to minimize differences in soil, climate, and fire regime. Aside from these factors, the sites were selected for their abundance of large termitaria (identified from aerial photographs). Data were collected on the size and species of woody plants found on mounds and in the surrounding matrix in May and June 2008, and functional trait data were recorded in April 2009 and May 2010.

Field methods

Forty pairs of mound and matrix sites were sampled for woody plant species. Mounds surveyed were >2 m tall or >10 m in diameter, with surface areas of at least 100 m^2, for comparison with adjacent matrix plots of similar size. The centre of the 10m radius matrix plot was placed 30 m from the mound in either a north,

south, west or east direction of the mound. The direction in each case was chosen at random using random numbers generated by a scientific calculator. North, east, south, and west were represented by the numbers 1, 2, 3, and 4 respectively (Makumbe 2008) A total of 15 termitaria-matrix sites were sampled in the Game Reserve (GR), 15 in the Bird Sanctuary (BS) and 10 on Glen Roy Farm (F).

Trait selection and measurement

I measured traits relating to a combination of the environmental filters of (1) disturbance and (2) plant protection from herbivory, using traits and data collection protocols outlined in Cornelissen et al. (2003). I also considered (3) specific functional traits previously used for miombo woody species across a gradient of herbivory (Richardson-Kageler 2004, table 4.1). To ensure that biological variation within each trait was of a comparable magnitude, I standardised the trait data to a mean of zero and a standard deviation of one (see Petchey and Gaston 2006). As traits were equally represented (table 4.1), weighting was not applied (Laliberté and Legendre 2010).

Data Analysis

Sampling adequacy

I compiled sample-based rarefaction curves for woody plant species assemblages on mounds and matrix for each of the 3 sites (Bird Sanctuary, n=15; Farm, n=10; Game Park, n=15) using EstimateS (Colwell 2006). I used the nonparametric Incidence Coverage Estimator (ICE) and Michaelis–Menten richness estimate to evaluate sample-size adequacy (Colwell and Coddington 1994). When ICE and Michaelis-Menten richness values converge closely at the highest observed values, sampling can be considered sufficient (Longino et al. 2002).

Table 4.1 . Woody plant functional traits for evaluating response to herbivory (adapted from Cornelissen et al (2003) and Richardson-Kageler (2004).

Woody plant trait b = binary (presence / absence) c = continuous, n = nominal o = ordinal	**Class**	**Trait information**
<u>Whole-plant traits</u> Growth form (n)	0,1- scrambler 0,1 – shrub 0,1 - tree	Adaptation to herbivory
Life form (n)	0,1 - phanerophyte 0.1, - chamaephyte	Survival likelihood
Plant height (c)	m	Fire and disturbance survival Correlates with rooting depth
Spinescence (b)	0,1 (presence / absence)	Herbivore defence Reduced drought stress
<u>Leaf traits</u> Leaf size (c)	mm^2	Leaf energy & water balance Influenced by nutrients & disturbance
Leaf palatability (o) (Walker 1980)	0 – unpalatable 1 – eaten but not selected 2 – palatable 3 - very palatable	Corresponds with: leaf strength leaf lifespan defence against herbivory
Phenology / 'Evergreeness'	direct measure (months)	leaf strength indirect protection from herbivory (strength may limit destruction)

Effect of position (mound vs. matrix) and herbivore treatment (BS vs. F vs. GP) on woody community species composition

To determine the overall effect of position (mound vs. matrix) and treatment site (BS vs. F vs. GR) on woody assemblage species composition, I first investigated differences in woody plant assemblages resulting from position (mound vs. matrix) for all sites combined, and then differences resulting from herbivore pressures (BS = exclusion, F = grazing, GP = browsing and mixed feeding) using an analysis of similarities (ANOSIM, Clarke and Warwick 1994). I explored the differences by constructing a similarity matrix for the woody plant species data set, using the Bray-Curtis similarity coefficient and sorting the data using group-averaging. Sites (BS, F, and GP) were used as grouping factors. Data were square-root transformed to reduce the influence of very abundant/common species (PRIMER v. 6, Clarke and Gorley 2006).

Influence of treatment and position (mound vs. matrix) on functional traits

The community-level weighted mean (CWM) is defined as the mean value for a trait within the community weighted by the relative abundance of the taxa having those values for the trait (Lavorel et al. 2008). Variation in the CWM of traits between assemblages can be informative when assessing ecosystem properties and community dynamics (Garnier et al. 2004, de Bello et al. 2005, Louault et al. 2005). I calculated the CWM for palatability, spinescence and phenology (the term "evergreeness" is employed in the text, as I used the binary classification 'evergreen' or 'deciduous' as measures of response to herbivory, for mound vs. matrix woody plants; see table 4.1). Instead of abundance, I used total biomass, since it would not be appropriate to consider small shrubs as equivalent to very large trees. I used height to estimate biomass of each species present in each plot, using an allometric equation derived by Higgins et al. (2007) for woody plants in the southern African bushveld: Biomass = 0.52 x height$^{2.55}$.

Influence of treatment and position (mound vs. matrix) on Functional Diversity

I used the functional traits listed in table 4.1 to assess FD. I identified functional groups by converting the species by trait matrix into a distance matrix using Gower distance. This allows individual traits to be

weighted differently (Podani 1999), and allows use of quantitative and qualitative traits together (Podani and Schmera 2006). I then clustered the matrix using unweighted pair-group method with arithmetic mean (UPGMA), which was chosen after checking for the highest cophenetic correlation (0.7 for UPGMA). Each species was therefore given a measure of similarity with every other species, based on the functional traits used (appendix 4.1).

For each plot I calculated the three primary functional diversity indices (Mason et al. 2005): functional richness (F_{Ric}, the volume of functional space occupied by the community), functional evenness (F_{Eve}, the regularity of distribution of abundance within functional space) and functional divergence (F_{Div}, divergence in the distribution of abundance in functional space; Villéger et al. 2008). These measures were calculated using the FD package in R (Laliberté and Shipley 2010).

Results

I recorded 10103 woody plants from 84 species (Bird Sanctuary (BS): mound, n = 3846 plants from 61 species and matrix, n = 1583 from 48 species; Farm (F): mound, n = 1196 from 41 species and matrix, n = 857 from 38 species; Game Park (GP): mound, n = 1757 from 47 species and matrix, n = 865 plants from 41 species, respectively). Michaelis-Menton and ICE estimators converged closely for the sample-based species rarefaction curves, indicating that sampling was sufficient (appendix 4.2).

Woody plant assemblages on mounds emerged as distinct from matrix assemblages (ANOSIM mound vs. matrix for all sites; n = 40, global r = 0.762, p = 0.001, fig. 4.3a). Between mounds from the different treatments (BS vs. F vs. GP), and between matrix plots from different treatments (BS vs. F vs. GR) woody plant assemblages were significantly different (table 4.2).

Table 4.2. Results of ANOSIM comparing effects of site (bird sanctuary vs. farm vs. game reserve) on woody composition for mounds (bird sanctuary n = 15, farm n = 10, game reserve n = 15; global R = 0.535) and matrix plots (global R = 0.291). Significance levels: ***, p<0.001; **, p<0.01

Site Comparison	**Mound**	**Matrix**
	R statistic	**R statistic**
bird sanctuary vs. farm	0.439***	0.252**
bird sanctuary vs. game reserve	0.637***	0.329***
farm vs. game reserve	0.477***	0.259**

Imposing the results produced by cluster analysis onto the ordination produced by multidimensional scaling confirmed the groupings (fig. 4.3b). Position (mound vs. matrix) influences assemblage composition to a greater degree than does treatment (bird sanctuary vs. game reserve vs. farm).

I found no significant difference in CWM for palatability between treatments (BS vs. F vs. GR; Kruskal-Wallis (K-W) rank sum test: K-W chi-squared = 4.17, d.f. = 2, p = 0.12). However, significant differences in palatability of woody species exist between mounds (greater palatability) and matrix (Wilcoxon rank sum test W = 66, p < 0.001).

Between matrix plots from the three sites, a significant difference in palatability was found for treatments (BS vs. F vs. GR; K-W rank sum test: K-W chi-squared = 10.1438, d.f. = 2, p = 0.006). When corrected for using post hoc Wilcoxon tests corrected with Bonferroni sequential corrections (Rice 1989), BS emerged as significantly more palatable than F, and significantly more palatable than GR. There was only weak support (Wild and Seber 1999) for differences in mound woody plant palatability between the different treatments (K-W chi-squared = 5.0422, d.f. = 2, p-value = 0.080; fig. 4.4a). Woody plants on mounds and matrix plots differed in leaf phenology (in this study I used degree of 'evergreeness'), which was greater for mounds (Wilcoxon rank sum test with continuity correction; W = 122, p < 0.001). Leaf phenology did not differ significantly between matrix plots for different treatments (BS vs. F vs. GR; K-W chi-squared = 2.6444, d.f. = 2, p-value = 0.267); nor between mounds (BS vs. F vs. GR; K-W chi-squared = 3.5366, d.f. = 2, p-value = 0.170; fig. 4.4b).

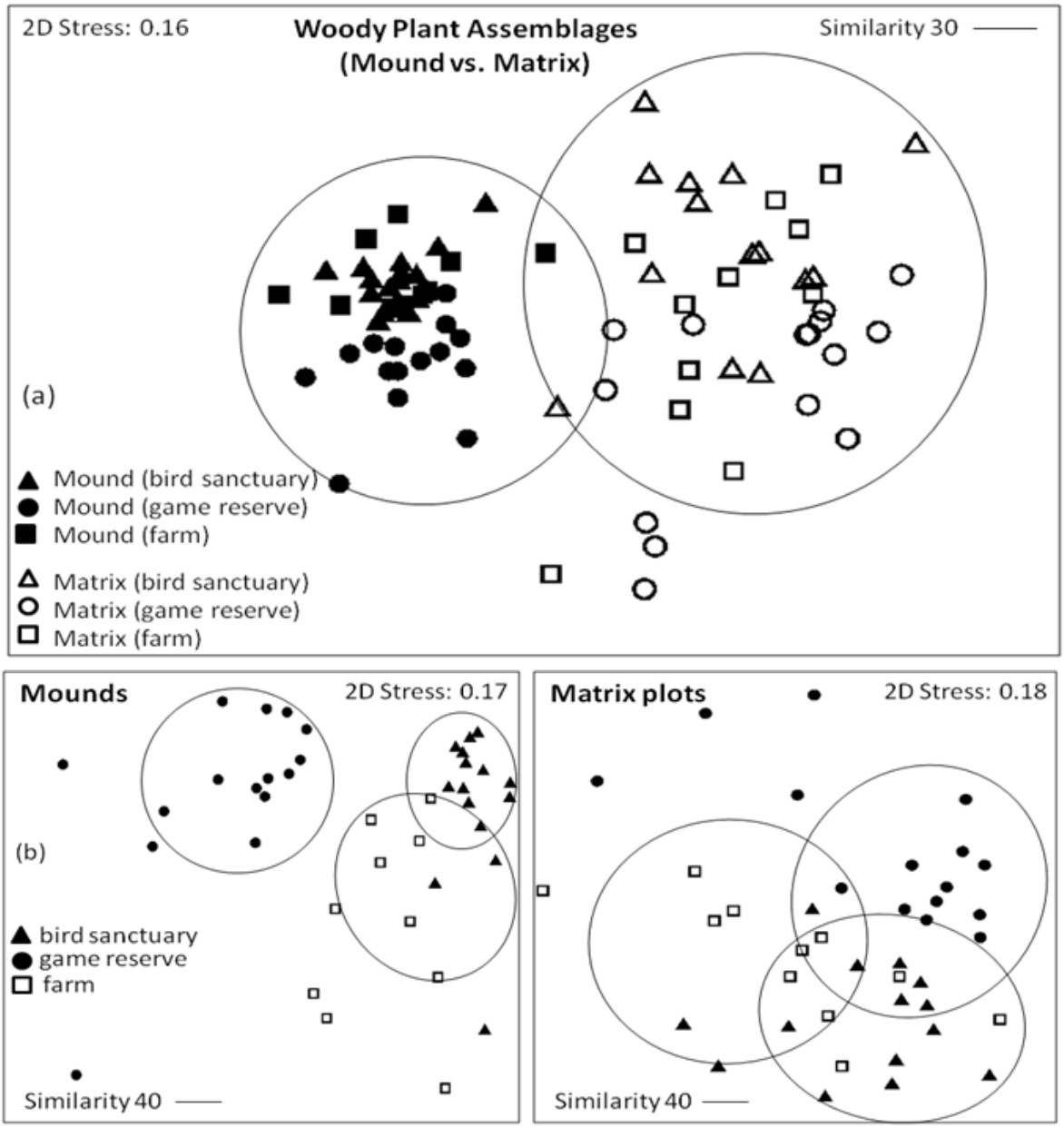

Figure 4.3. Ordination representing woody plant species assemblage for mound vs. matrix (a) at different sites (bird sanctuary, game reserve, farm). Groupings indicate assemblages similar by 30%. Mounds with differing herbivore exposure (bird sanctuary vs. game reserve vs. farm), and matrix plots with differing herbivore exposure were slightly more similar, and groupings indicate assemblages similar by 40% or more (b).

When comparing mound and matrix plots across all treatment sites, no significant difference existed for the trait 'spinescence' (Wilcoxon rank sum test; W = 875, p-value = 0.4734). However, 'spinescence' was significantly different between mounds for treatment sites (BS vs. F vs. GR; Kruskal-Wallis chi-squared = 13.0012, d.f. = 2, p-value = 0.0015), being lowest in the game park. Subsequent investigation using Bonferroni sequential corrections found no significant differences between the bird sanctuary and farm, but that the median of normalised values for spinescence on game farm mounds (-0.49599) was lower than both farm mounds (-0.27671), and bird sanctuary mounds (median: -0.19277). There was only weak support for the hypothesis that spinescence differed between matrix plots across treatments (Kruskal-Wallis chi-squared = 5.5732, d.f. = 2, p-value = 0.061; fig. 4.4c).

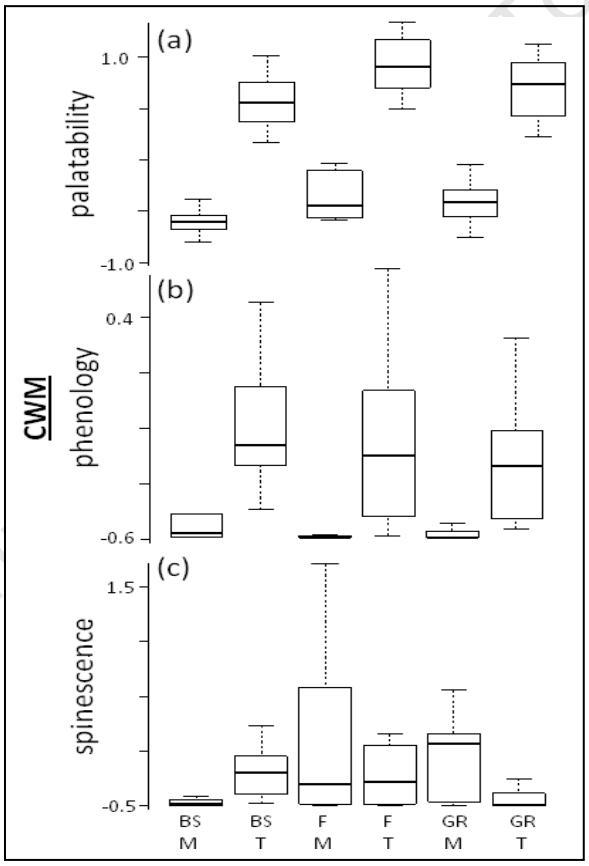

Figure 4.4. Comparison of the Community Weighted Means (CWM) of the traits 'palatability' (a), phenology (b), and spinescence (c) for matrix (M) vs. termitarium (T) across treatments (BS denotes bird sanctuary; F, farm and GR, game reserve).

F_{Ric} was significantly greater on mounds compared to the matrix (Wilcoxon rank sum test: W = 164, p-value < 0.001, mound median = 0.475, matrix median = 0.196). Highest values where recorded for the bird sanctuary, and lowest for the game reserve. F_{Ric} was significantly different between mounds across treatments (Kruskal-Wallis chi-squared = 20.914, d.f. = 2, p < 0.001; table 4.3). F_{Ric} was significantly lower for mounds in the game reserve than in the farm and bird sanctuary (medians: BS = 0.611, Farm = 0.466, GP = 0.353), but there were no significant differences between matrix plots under the different treatments (Kruskal-Wallis chi-squared = 3.145, d.f. = 2, p = 0.208).

Table 4.3. The three indices used to interrogate woody plant functional diversity under different exposures to herbivory: Functional richness (F_{Ric}), functional divergence (F_{Div}), and functional evenness (F_{Eve}).

		F_{Ric}	**Q_1; Q_3**	**F_{Div}**	**Q_1; Q_3**	**F_{Eve}**	**Q_1; Q_3**
Matrix	Bird Sanctuary	0.22	0.12; 0.35	0.62	0.55; 0.67	0.29	0.15; 0.43
	Farm	0.18	0.14; 0.27	0.60	0.52; 0.78	0.30	0.24; 0.34
	Game Reserve	0.11	0.05; 0.25	0.65	0.58; 0.76	0.33	0.20; 0.40
Mound	Bird Sanctuary	0.61	0.53; 0.71	0.87	0.81; 0.93	0.34	0.27; 0.46
	Farm	0.47	0.42; 0.59	0.91	0.89; 0.96	0.35	0.27; 0.44
	Game Reserve	0.35	0.24; 0.38	0.77	0.64; 0.89	0.28	0.17; 0.38

F_{Div} was significantly higher for mound plots than matrix plots (Wilcoxon rank sum test: W = 290, p-value < 0.001, medians: mound = 0.876, matrix = 0.648). F_{Div} also differed between mounds across treatments (Kruskal-Wallis chi-squared = 9.19, d.f. = 2, p = 0.01), with F_{Div} for mounds in the game reserve being significantly lower than those found on the farm. Mounds in the bird sanctuary did not differ significantly from either game park or farm (medians: farm = 0.907, game park = 0.773, bird sanctuary = 0.865. There was no significant difference between matrix plots (Kruskal-Wallis chi-squared = 1.603, d.f. = 2, p = 0.49)

F_{eve} did not differ significantly between mounds (Kruskal-Wallis chi-squared = 1.637, d.f. = 2, p = 0.441), nor between matrix plots (Kruskal-Wallis chi-squared = 0.146, d.f. = 2, p = 0.929) across treatments, and there was also no difference between mound and matrix plots overall (Wilcoxon rank sum test; W = 684, p = 0.268; medians and quartiles reported in table 4.3).

Discussion

My study supports the prediction that fine-scale spatial heterogeneity (in the form of large *Macrotermes* mounds) and disturbance (in the form of 40 years of differing herbivore exposure: browsing and mixed feeding vs. grazing vs. exclusion) can influence both the taxonomic and functional composition of woody plant assemblages in African savannas. Large termitaria emerge as foci of woody plant functional diversity, harbouring increased woody plant functional richness, and demonstrating the important role that spatial heterogeneity can play in disturbed systems. Overall, mound-associated woody plant communities formed distinct assemblages (fig. 4.3a), demonstrating the strong grouping effect of nutrient-rich mound soils, with altered hydrology and clay content that can influence establishment, growth and competition between plants, and hence facilitate the formation of distinct woody assemblages (Frost 1996, Konaté et al. 1999, Fleming and Loveridge 2003, Sileshi et al. 2010). Different types of herbivore exposure (BS vs. F vs. GP) resulted in three distinct mound-associated woody assemblages and matrix-associated assemblages, supporting the findings that browsing and mixed feeding vs. grazing affect woody plant species differently (Sankaran et al. 2008).

For both matrix and mounds, increased exposure to browsers resulted in lowered functional richness. By examining the community weighted means for traits that were linked to herbivory, it emerged that mound and matrix differed significantly with regard to woody plant palatability, and leaf phenology (represented by 'evergreeness' in this study), whilst spinescence was strongly influenced by type of herbivore treatment. Browsers select not only poorly defended palatable species, but also well defended species if they are adapted to the defence mechanism (e.g., giraffe feed on spinescent acacias

(du Toit et al. 1990, Skinner and Chimimba 2005)). Although leaf palatability was not significantly different across treatments (BS vs. F vs. GR), mound-associated trees emerged as palatability 'hotspots' when compared with matrix plots (Loveridge and Moe 2004, Mobæk et al. 2005), reflecting the effect of nutrient-enriched soils.

'Evergreenness' was not significantly different across treatments, but was higher for mounds than for matrix vegetation. Evergreen species photosynthesize year round and achieve early growth at the onset of the favourable season, before the deciduous species begin competition for light (Aerts 1995). 'Evergreenness' has associations to leaf strength (and thus protection from herbivores), and enriched, moist soils (Cornelissen et al. 2003, Jacobs et al. 2007). My results probably reflect both the eutrophic on-mound habitat and adaptation to herbivory.

Spines develop as defence in response to different, mostly vertebrate herbivores; they can also reduce heat and drought stress, and shelter non-spiny plants from herbivores (Cornelissen et al. 2003). Spinescence differed significantly between mounds of different treatments, and there was also weak support for matrix plots. For the matrix (which accounts for > 90% of area), spinescence was highest for the game reserve, intermediate for the farm, and lowest for the bird sanctuary, reflecting increased investment in defence from browsers. For mounds, findings were the exact opposite; lowest for GR, intermediate for F, and highest for BS, and seem to contradict the argument used above. However, browsing animals adapted to eating spinescent plants are present only in the game reserve, and as mounds can be herbivore 'hotspots', it is possible that foliage from spinescent palatables has been targeted, and that low spinescence perhaps reflects a tipping point at which the protective benefit of spines has been outweighed by the mound-intensive spatial distribution (untested in this study) of ungulate removal of highly-palatable spiny plants (Seif El Din and Obeid 1971, du Toit et al. 1990). Although I did not examine grass cover, it is also possible that competition with grasses may contribute to the higher levels of spinescence on farm termitaria, where overgrazing, in the absence of browsers, might release spiny woody species from the competitive constraints of grass (Bond and van Wilgen 1996, Scholes and Archer 1997, Higgins et al. 2000).

Higher functional divergence on mounds (F_{Div}) can suggest greater niche differentiation, which can result in lower competition between woody plant species for resources on such nutrient-enriched soils. (Mason et al. 2005) showed increased ecosystem function through better use of available resources. In our study, the elevated F_{Div} on mounds is likely to be related to another mechanism: as functional diversity is generally greater in nutrient rich systems, the probability of greater functional divergence is increased. For different treatment sites, matrix plots showed no differences in F_{Div}. For mounds, treatment affected F_{Div}, which was lowest in the browsing treatment. This lower divergence in the distribution of abundance of the chosen traits in functional space (Villéger et al. 2008) on browsed mounds implies a lowering of niche differentiation as a consequence of type of herbivory (Mason et al. 2005).

Functional richness (F_{Ric}) was higher overall on mounds. For mounds, across treatments, exposure to browsing decreased F_{Ric} (highest for BS, then F, and lowest for GR). The lowering of F_{Ric} suggests that not all resources available to the community are being used; the implication is that browsing may exclude some species, but also open additional niches (which in turn might increase future diversity). However, it can also mean that species adapted to benefit from such a situation may be missing, and increase the likelihood of invasive species exploiting the gaps in niche space (Tilman 1996, Dukes 2001).

Mason (2005) notes that F_{Div} relates to niche differentiation via competition for available resources, and I thus expected it would be higher in nutrient poor areas. In our study, this was not the case when comparing mound and matrix. Instead of observing a difference between the two (F_{Ric} and F_{Div}), they showed similar responses. This has implications for the interpretation of F_{Div}, and findings with regard to F_{Ric} and F_{Div} suggest that they might be corollaries in some circumstances (this study), but not in others (Mason 2005). In the vicinity of Lake Chivero there are two different forces, namely bottom-up processes associated with nutrient constraints, and top-down forces linked to herbivory. It is interesting to note that as browsing impacts on species at herbivory-hotspots (mounds), a decrease in both F_{Ric} and F_{Div} occurred. This again is contrary to expectation (which would have been for F_{Div} to increase as traits to avoid browsing become amplified). One explanation is that those species able to cope are so similar that they differ little in their functional traits. Another possibility is that nutrient constraints are so overwhelming

that F_{Ric} and F_{Div} always exhibit a similar pattern. This would imply that the bottom-up processes (soil nutrient driven) substantially outweigh the top-down effects of herbivory within this system, and in so doing mask more subtle changes.

Regardless of position (mound vs. matrix) and treatment, functional evenness (F_{Eve}) did not differ. Functional evenness may be viewed as a measure of how well the biomass of a community is distributed within niche space to enable effective use of the entire range of available resources, within the niche space that a given community occupies (Mason et al. 2005). High values for F_{Eve} equate to a very regular distribution of species' traits, whilst a low index suggests separate clumping of species, or their abundances, in niche space (Schleuter et al. 2010); Low values suggest that although some parts of niche space are occupied, they are under-utilized, with the net effect of decreasing productivity and reliability and increasing opportunity for invasive species (Mason et al. 2005). That F_{Ric} has changed between sites, whilst F_{Eve} has remained unchanged, has particular significance. Maintenance of functional evenness in the face of lowered functional richness shows that the communities contract in trait space by loss of similar functional types across treatments. In other words, the lower values for matrix sites and mounds in the game reserve suggest that woody assemblages have maintained the spread of traits, but that the abundance of these traits is diminished (i.e. trait abundance has been relatively reduced by browsing).

Although 40 years of exposure to herbivory is shorter than the lifespan of many woody plant species, exposure to browsing has altered assemblages and functional diversity. Mounds emerge as repositories of functional richness, and demonstrate the influence of spatial heterogeneity in the face of disturbance. For both matrix and mounds, increased exposure to browsers has lowered functional richness. For the system as a whole, maintenance of functional evenness in the face of lowered functional richness shows that woody plant communities have contracted in trait space by loss of similar functional types across treatments, implying a decrease in functional diversity and resilience of the miombo woodland's woody plant assemblage to intensive browsing.

This is not the final word; my findings expose a system that is designed to cope with disturbance. Browsing opens niche spaces as it selects for and potentially reduces the presence of certain species. This

can lead to an increase in niche possibilities, and select for well-adapted woody species of the future. However, when excessive browsing by wild ungulates begins to lower resilience, a future of increasing diversity can only emerge if the anticipated propagules are both present in the system, and have the opportunity to establish. Such events probably depend on the anticipated ungulate response to a system in need of rest (i.e., movement to greener pastures). This possibility becomes increasingly unlikely as curtailed migration becomes the norm. Chivero, like many other reserves in Africa, is surrounded by occupied land. In such a context, the question that next arises involves detecting at what point fence-lines and human populations foil the resilience of such herbivore-adapted woodlands and lead to irretrievable loss of ecosystem function.

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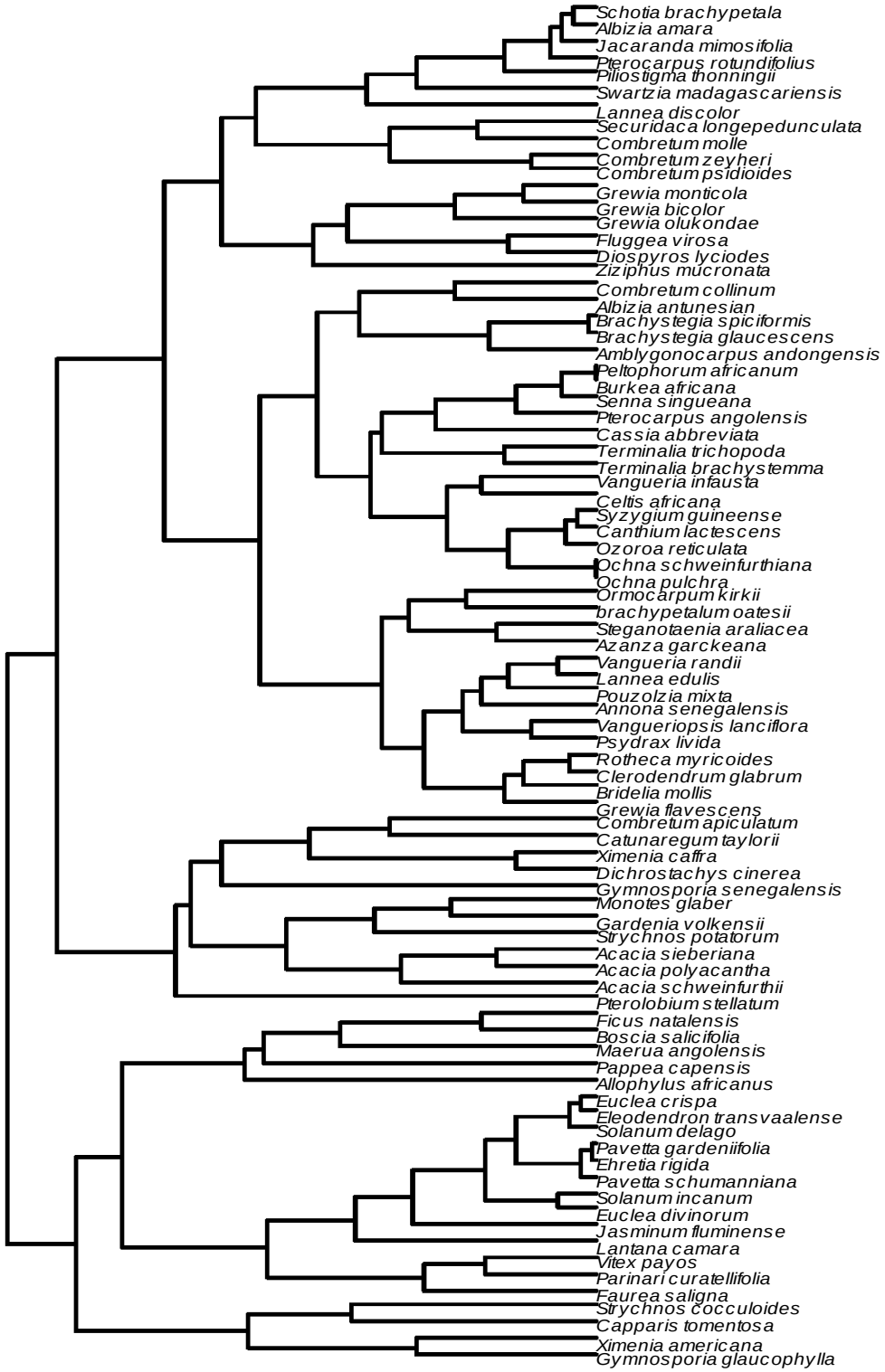
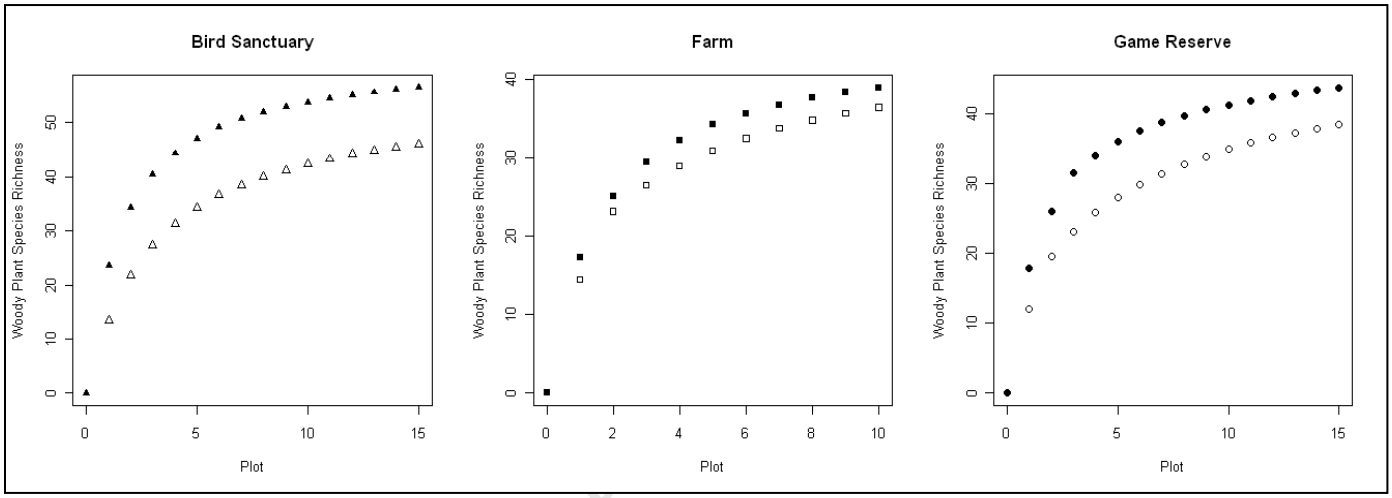
Appendices

Appendix 4.1. Woody plant functional groups based on functional traits collected in table 4.1



Appendix 4.2. Species accumulation curves; mounds are represented by symbols with a solid fill. For mounds: bird sanctuary $S = 26.852A^{0.3034}$; farm $S = 19.132A^{0.3362}$; game reserve $S = 17.544A^{0.3617}$. For matrix: bird sanctuary $S = 15.798A^{0.4315}$; farm $S = 12.767A^{0.4707}$; game reserve $S = 10.845A^{0.4912}$, where S = number of species observed and A = number of plots sampled.



5

Escaping the flames: large termitaria as refugia from fire in miombo woodland

Abstract

At finer scales, local heterogeneity can add complexity to fire regimes. Many studies mention differences in fire sensitivity between plants growing on termite mounds and the surrounding matrix, yet direct testing of fire-induced changes to woody plant species between the two habitats has received little attention. To test whether *Macrotermes* termitaria act as fire refugia for woody plants, I documented the effects of fire on individual plants, woody plant structure, and composition. The study took place in miombo woodland in Zimbabwe where high elephant densities have decreased tree canopy cover. This has led to an increase in grass cover, which can provide a substrate for fires to burn at greater intensity. I documented vegetation composition and structure on 47 mound-matrix pairs at three sites within the woodland, comparing mound and matrix for exposure to fire. Overall, mound-based woody plants were less exposed to fire than those in the matrix. Woody species composition differed between mound and matrix and there were significantly more tall trees on mounds. Only 10 mound-matrix pairs had been equally exposed to severe, late dry season fires. I subsampled all woody plant species on these 10 mound-matrix paired plots, recording grass cover, elephant damage, fire damage and resprouting response. Grass cover, important in fuelling fires, was three times greater in the matrix, where 85% of woody species experienced heavy fire damage, compared to 29% for mounds. For mound-matrix pairs that had experienced equal exposure to fire, woody matrix plants appeared better adapted to fire than mound plants, being nearly 31 times more likely to exhibit a vigorous resprouting response after fire damage, all else being equal. The unique suite of woody plants found on termitaria has generally been attributed to edaphic factors. To this may be added the fire-retardant properties of mounds (e.g., less grass, altered hydrology), which have allowed a distinct assemblage of woody species that resprout poorly after fire and might otherwise have been excluded, to persist in a fire-prone system. Studies show that termitaria harbour habitat for cavity-using birds, small vertebrates and arthropods; that trees growing on termitaria offer preferred forage to herbivores, and that termitaria increase primary, secondary and tertiary productivity. It follows then that the refuge effect from fire can be expected to have far reaching effects on overall diversity and productivity within the system.

Introduction

The spread of disturbance across a landscape can be influenced by spatial heterogeneity (Romme 1982, Turner 1987, Turner 1989). In particular, the spread of fire moving through a landscape can be influenced by landscape heterogeneity (Morvan *et al.* 1995), and landscape pattern (such as the degree of connectivity between flammable patches) can affect both initiation and spread of fire. For example, Clarke (2002) showed that some habitats within fire-prone vegetation can provide refugia for fire-sensitive species, reinforcing vegetation heterogeneity. When animal movement is restricted (as in reserves), mammals can play a principal role in the generation of heterogeneous patches through differential pressures (Farina 2006).

To examine how organism-generated spatial heterogeneity in the form of large *Macrotermes* termitaria mediates the effects of fire and herbivore disturbance, and to determine implications for woody plant diversity and future conservation efforts, I tested whether termitaria act as refugia from fire for woody plant species. The study sites in Chizarira National Park in north-west Zimbabwe contain *Macrotermes* mound at densities of 2 ha^{-1} (Joseph *et al.* 2011). They form part Africa's most extensive savanna woodland, the miombo system (Frost 1996), which covers 2.7 million km^2 (Millington *et al.* 1994). Macrotermitinae termitaria have emerged over the past decade as important foci for ecological research; they not only house a unique suite of woody plants, but can also harbour greater small vertebrate diversity and greater insect abundance (Fleming and Loveridge 2003, Pringle et al. 2010), provide habitat structure and nesting sites for cavity-using birds (Joseph *et al.* 2011), are important foraging sites for herbivores (Holdo and McDowell 2004, Loveridge and Moe 2004, Brody et al. 2010, Levick et al. 2010), and increase primary, secondary and tertiary productivity of systems (Pringle *et al.* 2010).

Chizarira is a mesic savanna with an mean annual precipitation (MAP) that generally exceeds 650 mm (differing areas range from 600 – 800 mm), so alteration of woody cover is likely to be driven by fire and herbivory, compared to arid savannas, which show a positive linear relationship between MAP and maximum woody cover (Bond et al. 2003, Sankaran et al. 2005). Soils in Chizarira are dystrophic, with low levels of N and P (Huntley 1982, Frost 1996). The park has harboured high elephant densities of >1

km^{-2} and at times as high as 3 km^{-2} (Cumming 1981, Dunham et al. 2006), and provides a good example of the increasingly common phenomenon of a converted woodland (as savanna woodland transforms to open grassland). Although the effect of fire intensity and frequency on savanna composition is variable (Scholes et al. 2003, van Wilgen et al. 2003), a decrease in canopy cover following elephant herbivory and tree felling can lead to an increase in grass cover (Barnes 1979, Mapaure 2001), that fuels hotter fires resulting in the system being caught in a fire trap (Frost 1996). The current condition of the woodland matrix is best explained by adopting the *Brachystegia* transition model (Starfield et al. 1993) which examines the relationship between fire, herbivory, and the woodland-bushland-grassland transformation, accounting for the expected synergistic effect between fire and elephant damage that can reinforce the transformation of woodland to grass- and shrubland. At low ignition probabilities, the model allows *Brachystegia* shrubs to grow despite elephant herbivory. At higher ignition probabilities, a combination of fire and elephant herbivory leads to suppression of *Brachystegia* shrubs and a switch to relatively fire resistant, bushy species. At very high ignition probabilities (which we observed in our study plots) hot fires occur, and the transition back to grassland occurs more frequently (fig. 5.1).

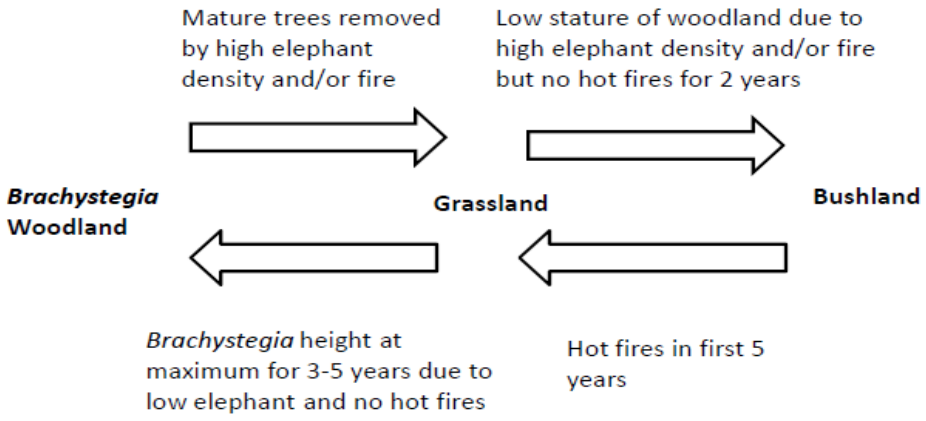


Figure 5.1. A summary of the *Brachystegia* transition model; adapted from Starfield *et al.* (1993)

Discussions of fire traps have tended to ignore fine-scale heterogeneity, such as that created by termite mounds. To date, the finding that large termite mounds harbour a distinct woody flora that is often taller than the surrounding matrix woodland has generally been ascribed to mound soil nutrients, clay content

and soil moisture (Fleming and Loveridge 2003, Moe et al. 2009). Termite activity concentrates nutrients and clay in mound soils, alters topography, changes mineral and organic soil composition, and affects hydrology and drainage (Fanshawe 1968, Wood and Sands 1978, Lal 1987, Jones et al. 1994, Schuurman and Dangerfield 1996, Dangerfield et al. 1998). These edaphic factors are clearly important, but the influence of fire on termitaria, which are unique and structurally important components of savanna woodland, has gone largely untested despite reference by a number of authors to possible reduced impact of fire on termitaria (e.g., Morison et al. 1948, Fanshawe 1968, Dangerfield et al. 1998, Barot et al. 1999, Bloesch 2008, Sileshi et al. 2010). Proposed mechanisms have included reduction in litter and grasses by termites, tree-grass competition that reduces grass cover, and the elevation of trees on mounds (Sileshi *et al.* 2010). Recently, Moe *et al*. (2009) found that many fire-sensitive species were restricted to mounds, but to date no study has directly quantified the effects of fire on the vegetation of termitaria

In this study, I asked whether large termitaria provide refugia from fire for woody vegetation; and if so, whether the refuge effect has influenced woody plant assemblage and structure. I address four overarching questions: (1) Are termitaria less exposed to fire? (2) Does the structure and composition of woody vegetation on and off mounds differ? (3) Do the relative degrees of fire and elephant damage reflect differing impacts of these two disturbances between on and off mound habitat? And (4) does the post-fire initial resprouting response of plants differ on and off mounds (see discussion by Nefabas and Gambiza 2007), reflecting different fire sensitivities?

Methods

Study site

Chizarira National Park (CNP) experiences a wet season from November to April, a cool dry season from May to July and a hot dry season from August to November. Mean annual temperature is 20 - 22.5°C (Torrance 1965). Mean annual rainfall is 600-800 mm (annual coefficient of variation of 25-30%, Lineham 1965).

Miombo is a broad-leaved deciduous woodland found on nutrient-poor soils, dominated by the Caesalpinioideae genera of *Brachystegia* and *Julbernardia* (White 1983, Frost 1996). In many parts of south-central Africa, including CNP, massive vegetated termitaria are constructed by *Macrotermes* (Isoptera). These mounds may be up to 9 m high with basal diameters of up to 30m (Malaisse 1978). Large termitaria create nutrient-rich patches within the miombo woodland. Since the 1970s, the impacts of elephants and fire have transformed most of the park's former tall, open woodland to shrubland (Thomson 1974, Cumming 1981) which is comprised mainly of regenerating *Brachystegia boehmii* and *Combretum* species in the matrix (fig. 5.2). Tall trees are confined to termitaria (Joseph *et al.* 2011).

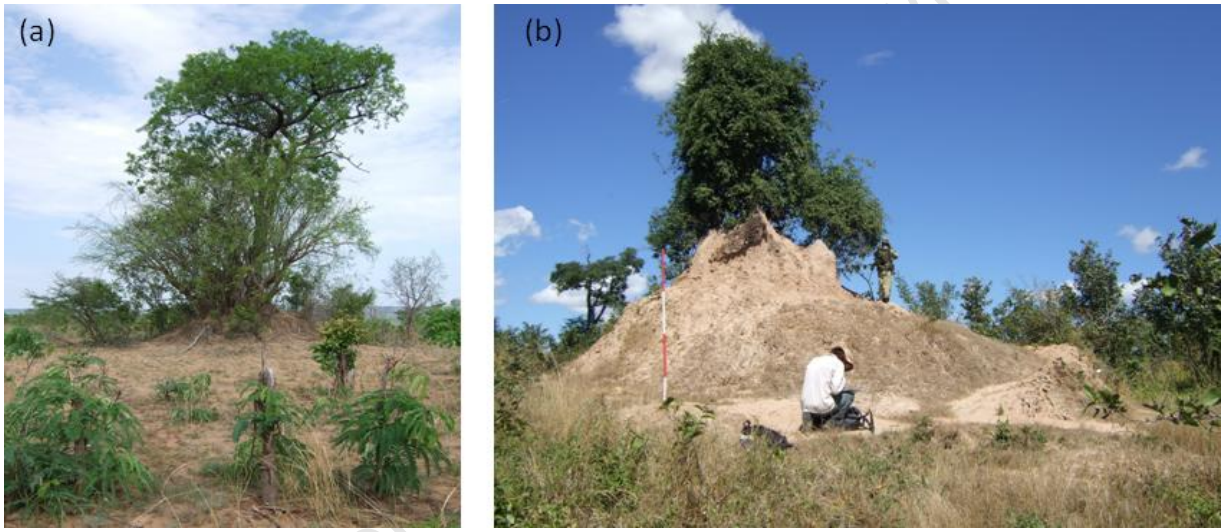


Figure 5.2. Tall trees characterise termitaria. Note the post-fire resprouting *Brachystegia boehmii* (which can grow to 15m) in the foreground (a). In this unburned plot, grass (an important substrate for fire) is visibly less prevalent on the termite mound than in the matrix (foreground, b).

Field Methods

Woody plant assemblages and grass cover on and off mounds

To assess species composition of woody plant assemblages, I surveyed 47 pairs of mound and matrix plots within three sites, in CNP, in November 2009. Mound surface areas of 100 m^2 were compared with adjacent matrix plots measuring 50 m by 2 m. Elongated matrix plots were used so as to better capture the habitat heterogeneity and potentially patchy disturbance effects within the matrix (Krebs 1999). Matrix

plots were set along randomly chosen compass bearings radiating out from the mound, starting 10 m from the mound perimeter. This survey represented a subset of a larger vegetation data set incorporating 63 mound-matrix pairs, which were surveyed previously in April 2009, and which had experienced no observable recent fire (i.e., within the last year) damage at that time. In the initial study, I recorded stem diameter at base and breast height, height, ramification (number of branches) and whether individual plants were living or dead. Subsequent fires affected 47 of the 63 pairs.

To assess woody plant community composition, all woody species were identified. To ascertain differences in vegetation height structure between on mound and off mound habitats, in addition to the height classes used for fire damage (see below), I recorded the number of trees > 6 m in height within all 47 paired plots. I measured percentage grass cover using the line-intercept method (Mueller-Dombois and Ellenberg 1974) over 50 m for both mound and matrix plots. As mounds measured less than 50 m in diameter, the line-intercept was repeated from a randomly-selected point on the circumference of the mound at least 3 m from the starting point of the first, and repeated until a total of 50 m of mound-surface had been surveyed.

Fire exposure for mound and matrix (presence / absence)

Of the original 63 mound-matrix pairs surveyed in April 2009, 47 pairs had been exposed to some degree of naturally-occurring fire damage (with presence of fire noted for either mound or matrix or both) by the time of the November 2009 survey. Fire damage to any plant (grass / shrub / tree) was taken as evidence of fire exposure for a particular plot. Total mound surface was compared with paired matrix plots measuring 50 m by 2 m. As all mounds had surface areas > 100 m^2 (calculated by modelling mound shape as a cone), ultimately, more mound area was surveyed than matrix area in this pilot study. Fires and their effects on vegetation are highly variable, owing to differences in fuel load, weather conditions, fire frequency, season and type of fire (Bond and van Wilgen 1996). To minimize the effect of this variability on my assessment of burning damage and resprouting response, I allocated fire damage ratings to each pair of the 47 mound-matrix plots (Fd_{plot}), as follows: 0 - no damage; 1- only grass burnt; 2- grass and

low shrubs <3 m burnt; 3 - trees burnt to a height of >3 m. Trees over 3 m become less susceptible to fire damage, while short trees often burn back to their base (Higgins et al. 2000, Furley et al. 2008). The Fd_{plot} rating was used to compare mound-matrix plots for degree of exposure to fire. Ultimately only rating level 1 was employed to differentiate presence / absence of fire for a given plot (i.e. an Fd_{plot} rated at 0 didn't burn; a burn at rating level of Fd_{plot} 1 or higher, denoted presence of fire)

Fire and elephant damage on mound and matrix vegetation (individual plants)

To control for the degree of fire exposure when examining effects at the level of individual plants, only plots burnt to Fd_{plot} level 3 were used to assess mound-matrix pairs that had undergone equal, and heavy exposure to fire. Pairs in which fire ratings differed between mound and matrix where excluded from the study for fire damage and resprouting to individual woody species. I identified ten mound-matrix pairs of Fd_{plot} rating 3 (i.e., fire damage had been inflicted on all height classes), within the original three sites (three at two of the sites, and four in the third), in which mounds were matched for catena, distance from drainage lines and water sources. The three sites were > 3 km apart and had burnt in three different fires. All fires covered an area > 500 m^2 (as documented by visual evidence of extent of damage to surrounding vegetation), and all had occurred at least 60 days prior to commencement of the study. I used these plots to assess fire damage, elephant damage, and resprouting responses in woody plants on and off mounds. I compared resprouting data to the pre-fire data for individual plants to ascertain new resprouting tissue and additional individual plant deaths after the initial survey. I attributed additional deaths to effects of fire.

For each mound and matrix plot, for all woody plants, I recorded species, height class (<1 m, 1-3 m, >3 m), individual woody plant fire rating (Fd_{plant}: 0: no sign of damage; 1: 1-20% of leaves burnt; 2: 20-100% of leaves burned and / or bark blackened; 3: bark cracked; 4: dead), resprouting response (0: no resprouting; 1: some resprout tissue (<10 cm); 2: >10 cm but <30 cm of resprouting tissue; 3: >30cm of resprouting tissue) and elephant damage rating (EDR). EDR was classified according to Anderson and Walker (1974); 0 = no damage, 1 = 1 – 10% of woody plant damaged, 2 = 11–25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-90%, 6 = 91-99%, 7 = 100%, i.e., dead. The inclusion of only mound-matrix pairs that had

experienced overall exposure to fires of similar intensities ensured that resprouting response for individual plants was normalized for fire effects.

Analysis

Comparison of species composition, tree structure and grass cover between mound and matrix plots

I explored species composition between matrix plots and large mounds using cluster analysis on a Bray-Curtis similarity matrix for woody plant species. Data were sorted using group-averaging and square-root transformed to reduce the influence of common species. I then compared woody plant assemblages on matrix plots with those on large mounds (n = 47) using an analysis of similarities (ANOSIM). These analyses were carried out using PRIMER v.6 (Clarke and Gorley 2001). For the 47 mound-matrix pairs, I assessed differences in density of trees > 6 m on mounds and in the matrix using a Wilcoxon matched pairs test. Similarly, comparison of grass cover for the subset of 10 mound-matrix pairs equally exposed to fire was assessed using Wilcoxon matched pairs tests.

Fire exposure for mound and matrix

For the 47 mound-matrix pairs, a chi-squared test (with Yates correction) was used to compare presence / absence of fire exposure, for mound vs. matrix plots.

Fire and elephant damage, and resprouting response, on mound and matrix vegetation

To test for differences in degree of elephant damage, fire damage (Fd_{plant}), and resprouting of woody plants between mound and matrix, I used a Kruskal-Wallis test, excluding dead individuals, as these could not be used to fairly represent elephant damage, or resprouting ability. These analyses were conducted in STATISTICA v. 9 (StatSoft 2008). Regarding fire and elephant damage, and resprouting response, the observational unit of the statistical analysis was the individual woody plant.

Since the resprouting response was ordinal (i.e., the measurements have relative instead of quantitative differences), I used ordinal logistic regression to assess the effects of position (mound *vs.* matrix), size class, site, and degree of fire and elephant damage and interactions between these explanatory variables

on resprouting response. The group of plants with elephant damage rating of 5 was small (n=5 in size class > 3 m), so I merged damage classes 4 and 5 to give a group of trees with damage levels of between 51% and 90%. Since the data behaved monotonically with explanatory variables (appendix 5.1), a proportional odds model was appropriate (Guisan and Harrell 2000). I used the R (R Development Core Team 2005) packages Design (Harrell 2009) and Hmisc (Harrell and contributions from many other users 2010) to conduct these analyses. I estimated bias and produced a bias-corrected estimate of the model using the bootstrap with resampling (Harrell *et al.* 1998), using 400 iterations. The model was validated using the maximum calibration error, which is the maximum difference between the predicted probabilities and the observed frequencies.

Results

Comparison of species composition, tree structure and grass cover between mound and matrix plots

Woody plant species assemblages on large termitaria were significantly different to those in the miombo woodland matrix (ANOSIM: global $R = 0.644$, $p = 0.001$, for large termitaria > 50 m^2 vs. matrix). The density of tall trees > 6 m on termitaria was far higher (n = 47, median = 34.61ha^{-1}) than for the surrounding woodland matrix (n = 47, median = 0 ha^{-1}, U = 651.000, p < 0.001). Grass cover was significantly higher in the woodland matrix than on mounds (mounds: median cover = 5.7%, Q_1 = 4%, Q_3 = 7, %, n = 10; matrix: median cover = 15%, Q_1 = 12.6%, Q_3= 20.4 %; Wilcoxon matched pairs test: p < 0.01; n = 10; fig. 5.3).

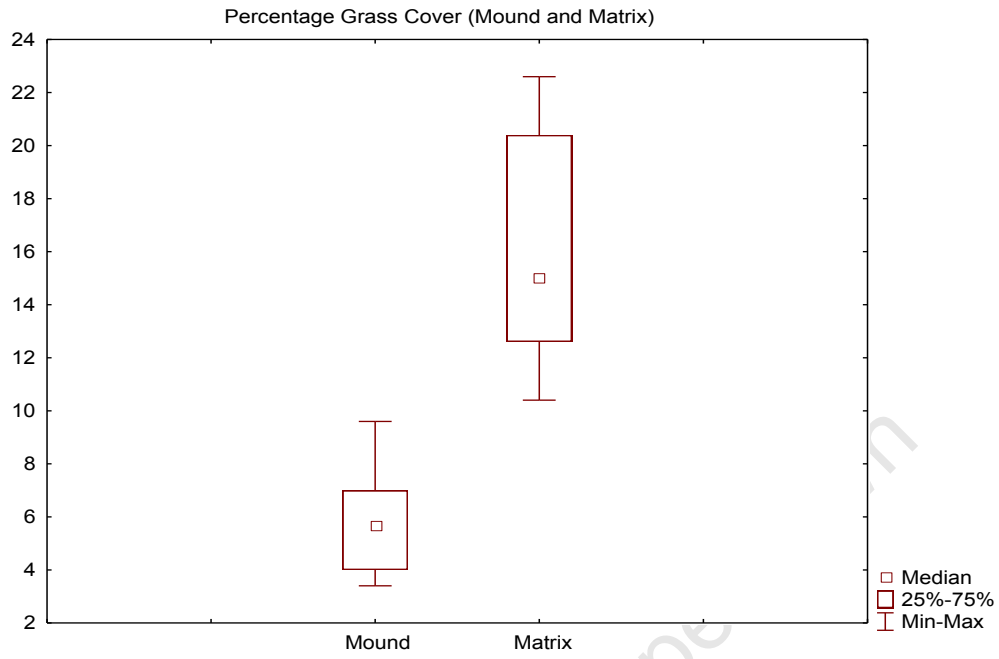


Figure 5.3. Percentage grass cover on large termitaria and in the woodland matrix.

Fire exposure for mound and matrix (presence / absence)

Mounds had been significantly less exposed to fire than matrix plots ($\chi^2 = 14.19$, df = 1, $p < 0.01$). Of 47 surveyed mound-matrix pairs, 37 matrix plots (79%) had evidence of fire damage. Only 18 mounds (38%) had experienced exposure to fire, and all 18 paired matrix plots also showed fire damage.

Fire and elephant damage, and resprouting response, on mound and matrix vegetation (individual plants)

Amongst the mounds surveyed for fire and resprouting, there were 1600 woody plants (1213 and 387 on mounds and matrix, respectively). Of these, 66 matrix and 11 mound trees had been killed by fire.

Mean ranks of elephant damage (H = 77.63, 1 d.f., $p < 0.001$), fire damage (H = 449.97, 1 d.f., $p < 0.001$), and resprouting (H = 481.07, 1 d.f., $p < 0.001$) were significantly different between mound and matrix woody plants (all height classes, n = 1523, Kruskal-Wallis). Woody plants on mounds experienced greater elephant damage, but woody plants in the matrix experienced greater fire damage (fig. 5.4).

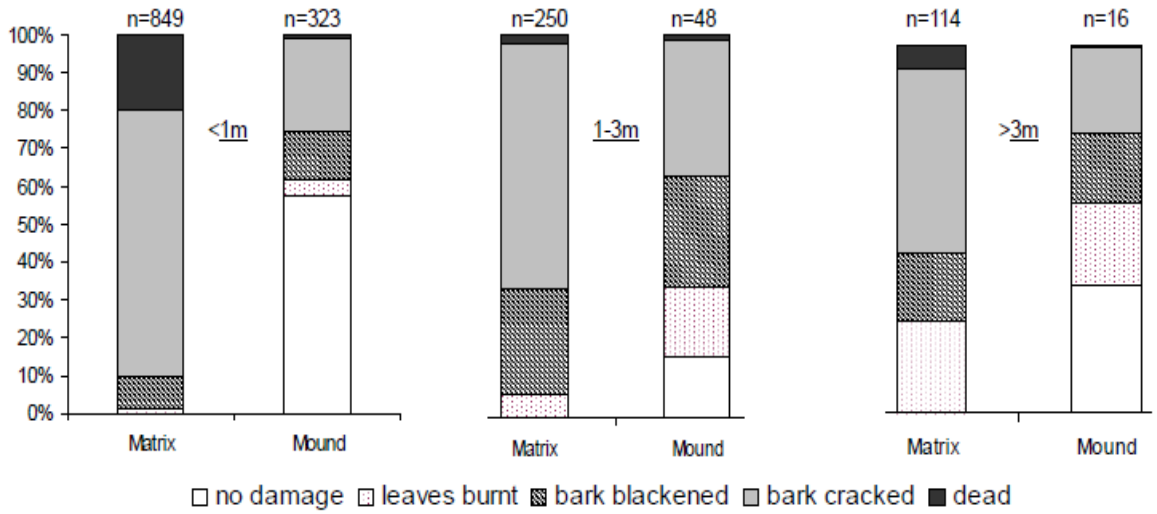


Figure 5.4. Differential exposure to fire for different height classes. The proportion of woody plants damaged by fire on mounds is lower than in the woodland matrix for all height classes (<1m, 1-3m, and >3m).

Just under 3% of woody plants in the matrix exhibited low levels of fire damage (i.e., 1 or 0), compared to 54.2% of woody plants on the mound (table 5.1; fig. 5.4). In contrast, 68.7% of woody plants in the matrix had been severely burned (i.e., damage level 3), compared to 28.5% of plants on mounds, with over 17% being killed by fire (level 4) in the matrix, compared to less than 1% of woody plants growing on mounds.

Resprouting response was significantly related to position (i.e., mound vs. matrix), size class, fire damage rating and elephant damage rating (Ordinal logistic regression: Chi-square likelihood ratio = 943.14, d.f. = 6; corrected pseudo $R^2 = 0.538$, corrected Somer's $D_{xy} = 0.76$, $p < 0.001$). There were no significant interactions. Resampling with replacement found the maximum calibration error (the maximum difference between predicted and observed frequencies) of the predicted resprouting response to be 0.0028, which is low and therefore suggests that the model is satisfactory. Plants on mounds showed a lower resprouting response, and resprouting response increased with size class, fire rating and elephant damage ratings. Site had no significant effect on the outcome (table 5.2).

Table 5.1. Fire damage to individual woody plants (expressed as total number, and as a percentage of the total) as a function of site (matrix vs. mound).

Fire damage rating	**MATRIX**		**MOUND**	
	Number of woody plants	Percentage of woody plants	Number of woody plants	Percentage of woody plants
0	0	0	554	45.7
1	11	2.8	104	8.6
2	44	11.4	198	16.3
3	266	68.7	346	28.5
4	66	17.1	11	0.9
Total	**387**		**1213**	

Mound plants were significantly negatively associated with resprouting response, with an expected log odds change of -3.44, or a 0.03 chance of plants on mounds resprouting, compared to their matrix counterparts. In other words, plants in the matrix are 31 times more likely to show a more vigorous resprouting response than mound plants, all else (i.e., size class, fire damage and elephant damage) being equal. For a one unit increase in size class, the expected ordered log odds increase is 1.07. For example, a tree less than 3 m high is 2.91 (i.e., $e^{1.05}$) times more likely to show a greater sprouting response than a tree less than 1m high (table 5.2).

Table 5.2. All predictors included in the proportional odds model were significant, but interactions were not: resprouting is greater in the matrix, and response increases with larger tree size, degree of fire damage, and elephant damage.

	Coefficient (log odds ratio)	S.E.	Odds Ratio	Wald Z	Chi-Square	d.f.	*p*
Position: Mound	-3.44	0.186	0.03	-18.47	341.20	1	< 0.001
Size Class	1.07	0.100	2.91	10.74	115.30	1	< 0.001
Fire damage rating	0.66	0.076	1.93	8.72	75.95	1	< 0.001
Elephant damage rating	0.41	0.053	1.51	7.87	61.87	1	< 0.001
Site 2	0.029	0.150	1.03	0.19	3.62	2	0.16
Site 3	0.30	0.170	1.35	1.74			
TOTAL					540.42	6	< 0.001

Similarly, fire damage rating with a log odds increase of 0.66 indicates that a tree with a fire damage rating of 2 is 1.93 times more likely to exhibit a greater sprouting response than a tree with a fire damage rating of 1 (fig. 5.5 illustrates this trend). The results of the model are supported by the observation that mean resprouting response increased with an increase in fire damage only for woody species in the matrix (fig. 5.5).

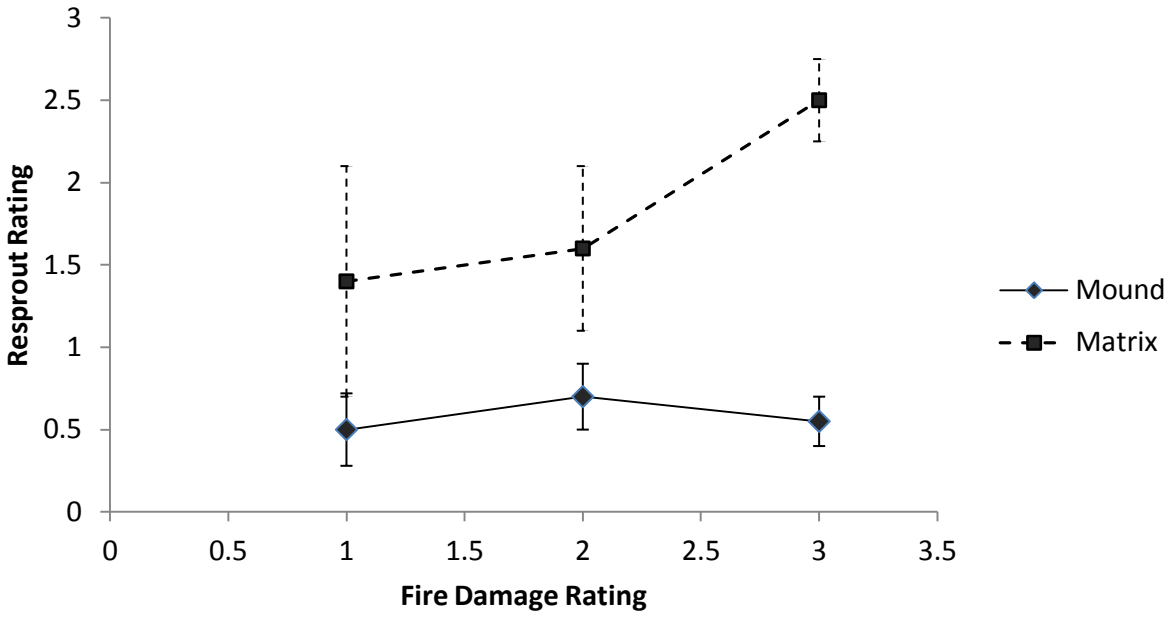


Figure 5.5. Matrix tree species exhibit greater mean resprouting response with increasing fire damage, whereas this response is absent for on-mound tree species across size classes (whiskers denote standard deviation).

It thus appears that trees on mounds experience less fire damage and are poorer resprouters than matrix tree species, which experience more fire and are good post-fire resprouters. These findings are supported by comparison of resprouting response and fire damage for individual tree species (table 5.3).

Table 5.3. Mean fire damage ratings and resprouting indices for those species that occurred in more than 80% of mound or matrix plots. Matrix trees undergo greater fire damage, and resprout with more vigour.

Mound woody plant family and species	Mean fire damage (0	Mean resprout (0	**Matrix woody plant family and species**	Mean fire damage (0	Mean resprout (0
Anacardiaceae			**Anacardiaceae**		
Lannea schweinfurthii	1.6 ± 1.3	0.7 ± 0.7	*Sclerocarya caffra*	3.0 ± 0.0	1.0 ± 0.0
Annonaceae			**Apocynaceae**		
Friesodielsia obovata	2.0 ± 0.9	0.7 ± 0.8	*Diplorhynchus condylocarpon*	2.5 ± 1.2	2.2 ± 0.9
Bignoniaceae			**Combretaceae**		
Markhamia zanzibarica	1.7 ± 1.5	0.0 ± 0.0	*Combretum apiculatum*	2.8 ± 0.6	2.0 ± 0.9
Burseraceae			*Terminalia brachystemma*	3.0 ± 0.0	3.0 ± 0.0
Commiphora mollis	2.2 ± 1.0	1.0 ± 1.0	**Euphorbiaceae**		
Capparaceae			*Bridelia cathartica*	3.0 ± 0.0	2.0 ± 0.0
Capparis tomentosa	0.8 ± 1.1	0.8 ± 1.2	*Pseudolachnostylis maprouneifolia*	1.8 ± 1.0	2.8 ± 0.5
Maerua prittwizii	0.0 ± 0.3	0.0 ± 0.0	**Fabaceae-Caesalpinioideae**		
Combretaceae			*Brachystegia boehmii*	2.4 ± 0.6	2.3 ± 0.8
Combretum mossambicense	1.9 ± 1.1	0.3 ± 0.8	*Brachystegia spiciformis*	2.7 ± 0.6	2.3 ± 1.2
Ebenaceae			*Julbernardia globiflora*	2.9 ± 0.4	2.4 ± 0.8
Diospyros kirkii	2.1 ± 1.2	1.8 ± 1.1	**Fabaceae-Papilionoideae**		
Diospyros mespiliformis	1.0 ± 1.2	0.8 ± 1.5	*Dalbergia melanoxylon*	2.8 ± 0.6	0.8 ± 0.6
Diospyros quiloensis	2.2 ± 1.1	0.2 ± 0.4	*Pericopsis angolensis*	3.0 ± 0.0	3.0 ± 0.0
Diospyros senensis	1.9 ± 1.5	0.1 ± 0.4	*Pterocarpus rotundifolius*	2.8 ± 0.4	2.2 ± 1.0
Euclea divinorum	1.1 ± 1.0	0.7 ± 1.0	*Xeroderris stuhlmanni*	2.2 ± 0.8	0.9 ± 0.5
Euphorbiaceae			**Flacourtiaceae**		
Flueggea virosa	1.7 ± 1.3	0.1 ± 0.4	*Flacourtia indica*	2.4 ± 0.9	2.8 ± 0.4
Fabaceae-Caesalpinioideae			**Rubiaceae**		
Colophospermum mopane	2.6 ± 0.7	1.3 ± 0.9	*Catunaregam taylorii*	3.2 ± 0.4	0.7 ± 0.6
Fabaceae-Mimosoideae			*Crossopteryx febrifuga*	3.0 ± 0.0	3.0 ± 0.0
Acacia nilotica	2.3 ± 1.0	0.9 ± 1.0	**Tiliaceae**		
Rubiaceae			*Grewia bicolor*	3.0 ± 0.0	1.0 ± 0.0
Feretia aeruginescens	2.4 ± 1.1	0.1 ± 0.3			
Sapotaceae					
Manilkara mochisia	0.6 ± 1.1	0.5 ± 0.8			

Discussion

The effects of fire on woody plants, and the responses of woody plants to fire differed markedly at the scale of termitarium vs. matrix within the landscape. Overall (for all 47 plots), mounds where less exposed to fire. In the 10 matched plots where mound-matrix pairs experienced equal exposure to fire, woody plants on mounds were less damaged by fire than their matrix counterparts. The vast majority (85%) of woody plants in the matrix experienced severe fire damage, compared to just under 30% of woody plants on mounds. Moreover, matrix plants were more than 30 times more likely to exhibit a higher level of resprouting response to fire than their mound counterparts, all else being equal (table 5.2). It is important to note that this statistic deals with 'likelihood' of showing a higher resprouting response, and is very different to an 'average' resprouting response (for example, for a matrix plant, the chances of resprouting to level 2 is 30 times that of a mound plant – which would resprout to level 1).

Resprouting response was also positively associated with size class, fire damage and elephant damage rating. Similar findings have been made regarding coppice regeneration, in which taller stumps show a greater response (Mushove and Makoni 1993), possibly because individuals within larger size classes have access to greater physiological resources and so are able to resprout more vigorously (almost 3 times more likely in this study). Likewise, at each successive category of increased fire damage, the chance of exhibiting a higher resprouting response was nearly doubled. This result is consistent with the findings of Nefabas and Gambiza (2007) and further supports their hypothesis that vigorous resprouting is an adaptation to fire for trees in miombo woodland systems.

Woody plant species composition on termitaria was distinct from that of the woodland matrix, as previously described by other studies (e.g., Fleming and Loveridge 2003, Moe et al. 2009). Termitaria differ as a habitat from the woodland matrix because of higher nutrient and clay content in their soils (Dangerfield 1991, Frost 1996, Holdo and McDowell 2004), and (it emerges here), also because of decreased exposure to fire. Concomitant with reduced exposure to fire on these habitat islands was a higher incidence of plants that did not resprout well compared to the surrounding matrix, as has been observed elsewhere (Bond et al. 1988, Clarke 2002). Thus, mounds support a different suite of less fire-

exposed and less fire-adapted woody plant species relative to the matrix. These mound-associated species have been found to be important components of the woodland, serving as browse and habitat for a range of miombo woodland faunal species (Fleming and Loveridge 2003, Loveridge and Moe 2004, Joseph et al. 2011).

In addition to finding a distinct suite of species on mounds compared to the matrix, I found that trees > 6 m persist in the system primarily on mounds (also noted by Fleming and Loveridge 2003). The effect is so marked in the field that mounds in Chizarira are recognised from a great distance by their associated tall woody plant structure, which contrasts with the receding matrix woodland. Termitaria and their associated vegetation probably escape fire in a number of ways including (1) reduced grass cover, which limits fuel supply to high intensity fires (in our study, grass cover was almost three times lower on termitaria than in the matrix, consistent with findings for termitaria in West African savannas; Konaté *et al.* 1999); (2) shade from termitarium trees has variable effects on grassy cover, but together with competition from woody plants, can decrease cover (Belsky 1994); (3) soils of *Macrotermes* mounds may prove less hospitable to short-rooted grasses with their altered clay, silt, and mineral content relative to the grassy matrix; (4) within the study site, most mounds were at least partially circumscribed by large "halos" (often many metres in width) of eroded soil that support little vegetation, which may act as natural firebreaks; (5) soils of *Macrotermes* termitaria may be higher in moisture content because of greater clay content, which has good water-holding capacity (see chapter 2); (6) the foraging action of termites themselves can lower the fuel load (litter, as *Macrotermes* are not herbivorous) on and around termitaria (Dangerfield *et al.* 1998); (7) more intense grazing by ungulates on mounds (Mobæk et al. 2005); and lastly, (8) termitaria are elevated above the surrounding matrix, which may further exclude fire (Moe et al. 2009, Sileshi et al. 2010).

Phylogenetic differences exist between mound-matrix tree communities, demonstrating that in some instance fire-adaptation can be a phyogenetically conserved response. For example, the families Ebenaceae and Capparaceae had mound affiliations, whist Papilionoideae, and to a lesser extent the sub-family Caesalpinioideae, were more common in the matrix (table 5.3). Given the potential for a difference

in fuel load, weather conditions, season, ground moisture, and plant structure, replicates of natural burns (and even those in controlled plots) are very difficult to achieve. Replication was achieved by examining three different fires. Individual plants were documented pre and post burn for assessment of mortality. As comparison of initial resprouting response was tested, further replication is unlikely to have altered the outcome. A combination of very significant results and supporting field observations reinforce the findings.

At broader scales, and keeping in mind that the study site is mesic savanna (MAP up to 800mm yr^{-1}) in which woody structure can be expected to be strongly influenced by the disturbance regimes of fire, and to a lesser degree by herbivory and soils (Sankaran *et al.* 2005), Chizarira's woodland behaves as expected in the face of current levels of fire and herbivory. Over the past 3 decades, woody structure has declined markedly within the woodland matrix of Chizarira National Park. Whereas termitaria act to exclude fire, the converted miombo woodland matrix of Chizarira National Park, which has harboured elephant densities of up to $3.km^{-2}$, has the potential to be caught in a fire trap. With fluctuating elephant densities and CNP ranger reports (pers. comm.) of increased fire-setting by poachers, the system is by no means in equilibrium. At this point, elephant herbivory has opened up the woodland and the resultant increase in grass cover (mostly unpalatable *Hyparrhenia*) has facilitated the frequent and hot fires observed, causing further thinning of the woodland and further increase in the grass component.

Frequent, hot fires, combined with ongoing elephant herbivory, have previously been identified as preventing the regeneration of miombo woodland. Thomson (1974) documented a cycle of high density elephant herbivory and fire, leading to a loss of 20% of trees per year; by 1981, the woodland in his study had all but disappeared (Cumming 1981). Sengwa Wildlife Research Area (which is adjacent to my study site) also experienced a decrease in miombo woody cover from 95.2% in 1959 to 62.9% by 1983 in the setting of high elephant numbers and fire (Mapaure and Campbell 2002).

Tree species on termitaria appear to have been spared. Despite the potential matrix fire trap, I found that tall trees > 6 m in height persist in the system; and most occur on mounds (as noted by Fleming and Loveridge 2003). As a consequence of escaping the flames of the fire trap, on-mound tree species

(which are less fire-adapted) can attain the necessary height and girth which can provide protection from fire (Gignoux et al. 1997, Higgins et al. 2000, Nefabas and Gambiza 2007, Levick et al. 2009). Ultimately, termitaria provide a microhabitat for a fire-sensitive suite of woody species (fig. 5.6).

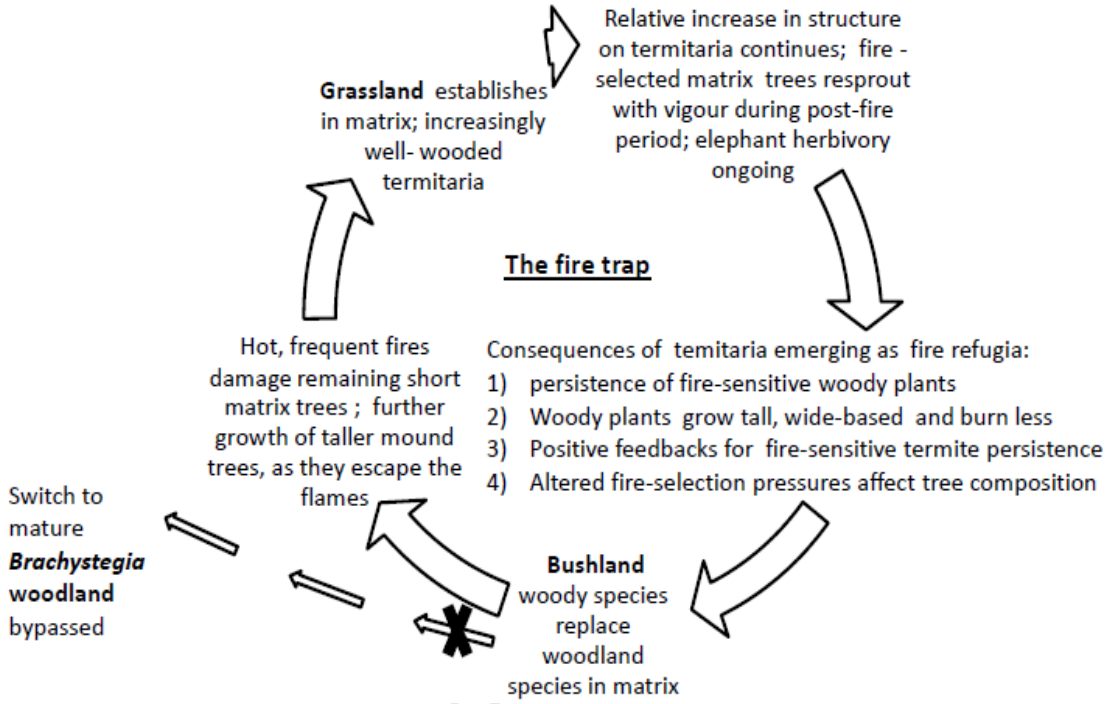
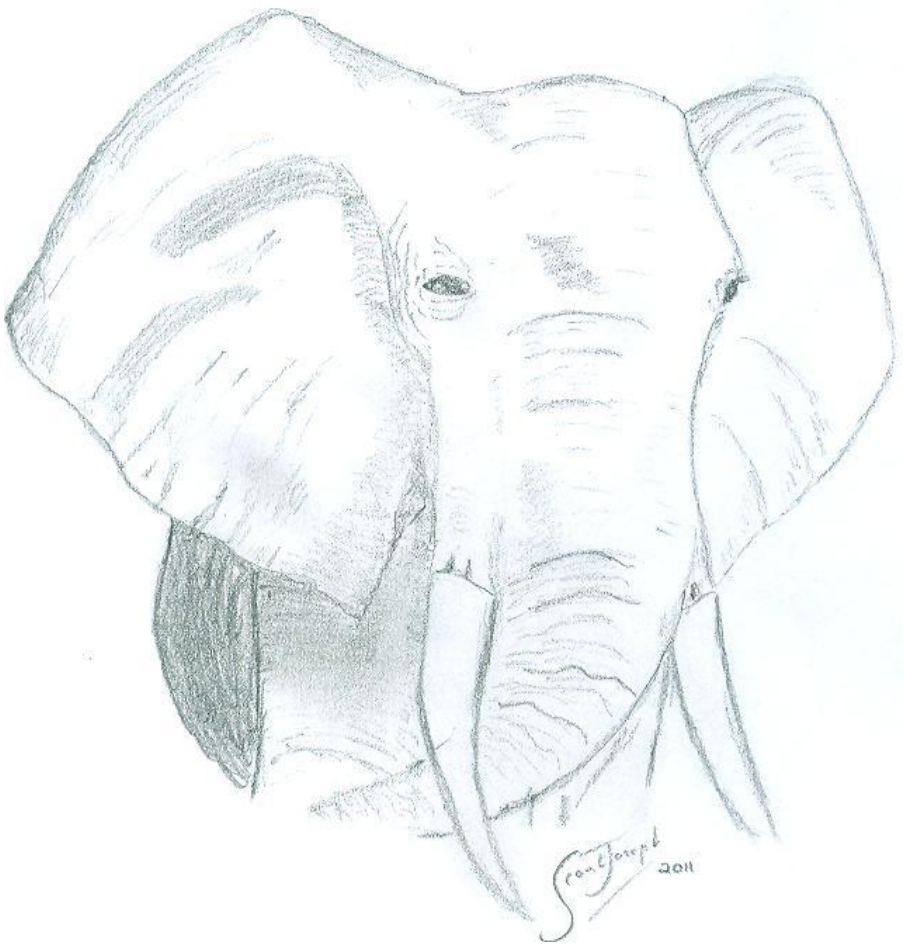


Figure 5.6. Despite elephant- and fire-induced conversion of *Brachystegia* woodland to grassland, termitaria preserve tree structure and allow fire-sensitive species to remain in the system.

Results suggest that through provision of nutrient-rich soils and refugia from fire, termitaria offer a niche for a suite of woody species that might otherwise not have persisted in a dystrophic system with frequent fires. Research that identifies biologically diverse patches, capturing the scale of the patterns and processes that add such diversity, allows for the concentrated focus of conservation efforts at a time of constrained financial resources. Termitaria emerge as profoundly important areas for many elements of biodiversity through their provision of sources of forage (Holdo and McDowell 2004, Loveridge and Moe 2004, Mobæk et al. 2005, Brody et al. 2010, Levick et al. 2010), habitat for a wide range of animals

(Fleming and Loveridge 2003, Joseph et al. 2011), and in their role as refugia for propagules, colonizers, and functionally important organisms (e.g., seed-dispersing and pollinating animals) following disturbances. Whether these ecological roles of termitaria have a broader-scale impact on tree to grass ratios and net primary production across the entire miombo system remains to be seen.



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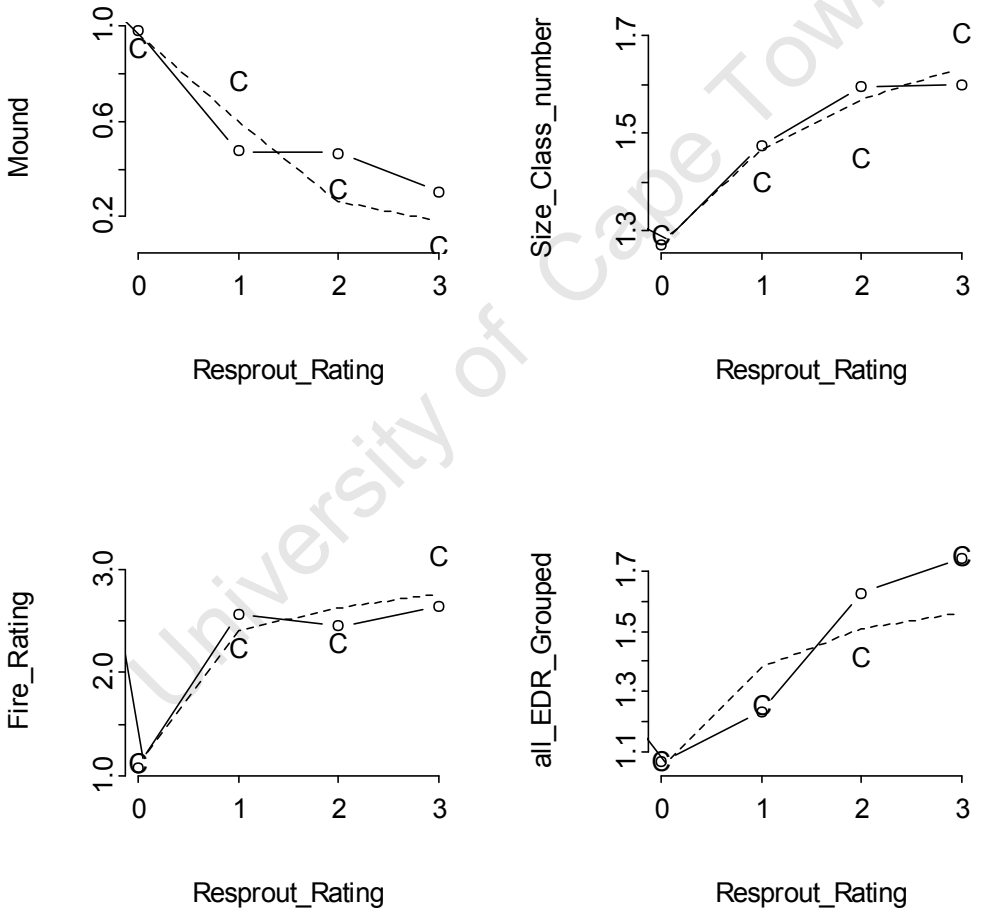
Appendix

Appendix 5.1. Graphical exploration of data to assess whether application of the Proportional Odds (PO) model is appropriate. Means of all potential predictors were calculated for each ordinal response class and plotted against it. The plain line indicates the fit of the PO model, the dotted line with a series of "C" labels indicates the fit of the Continuation Ratio (CR) model. Ordinality is satisfied for both PO and CR models, showing an overall monotonic trend (see Guisan and Harrell 2000 for more details).



6

Large termitaria as refugia for tall trees, deadwood and cavity-using birds in a miombo woodland

Abstract

Landscape heterogeneity can play an important role in providing refugia and sustaining biodiversity in disturbed landscapes. Large *Macrotermes* (Isoptera) termite mounds in miombo woodlands form nutrient rich islands that sustain a different suite of woody plant species relative to the woodland matrix. I investigated the role of termitaria in providing habitat for cavity-using birds in miombo woodlands that had been greatly impacted by elephants and fire, by comparing the availability of habitat favoured by cavity-using birds (tall trees, trees with deadwood, and cavities) on and off mounds, and then testing its effect on species richness and abundance of cavity-using birds. I surveyed 48 termitaria paired with 48 woodland matrix sites in the breeding season; and 54 matrix-termitarium pairs in the non-breeding season in Chizarira National Park, Zimbabwe. Generalized linear mixed-effects models showed that termitaria harboured significantly higher densities of tall trees, trees with deadwood, and cavities. A model selection procedure showed that termitaria provided refugia for cavity-using birds and contributed to the resilience of bird communities through high on-mound densities of trees with deadwood. Large termitaria thus appear to play an important role in maintaining functionally important components of the avifauna in heavily impacted Miombo woodlands.

Introduction

The action of ecosystem engineers, "organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials" (1994; page 374), is one of the more dynamic sources of spatial heterogeneity within landscapes. This activity can influence habitat heterogeneity, resilience (Dangerfield et al. 1998), and biodiversity within a given ecosystem (Yair and Rutin 1981, Jones et al. 1994).

In southern African savanna woodlands, two of the most widely acknowledged ecosystem engineers are elephants and mound-building termites. Both are capable of altering the distribution of nutrients across a landscape as well as influencing the nature and intensity of flows of nutrients within and between different parts of the landscape. However, their broader synergistic impacts on other components of biodiversity are poorly understood. Elephants and termites interact directly (elephants frequently destroy mounds for minerals and during foraging) and indirectly through landscape-level disturbance regimes. Intensive elephant herbivory can reduce tree canopy cover, with a concomitant increase in grass biomass, fuelling more frequent or intense fires (Guy 1989, Dublin et al. 1990, Mapaure 2001), ultimately resulting in the conversion of woodland to grassland or shrubland that largely lacks tall trees (Cumming et al. 1997, Mapaure 2001).

Termites of the genus *Macrotermes*, through mound and subterranean gallery construction and soil particle redistribution, alter mineral and organic soil composition, topography, hydrology and drainage, and nutrient flow rates which can ultimately influence vegetation and regional biodiversity (Wood and Sands 1978, Lal 1987, Jones et al. 1994, Schuurman and Dangerfield 1996, Dangerfield et al. 1998). For example, in a study in Uganda, Moe et al. (2009) found significantly higher numbers of woody species and densities of trees on termitaria, compared to the matrix. In Zimbabwe, Fleming and Loveridge (2003) reported that termitaria in a miombo woodland supported distinct plant assemblages and higher levels of small mammal diversity compared to the matrix. They hypothesized that this impact was due principally to the increased heterogeneity that mounds create in the woodland. In this study, I consider the

effects that two groups noted for their ability to engineer ecosystem change, namely termites and elephants, have on a third group of ecosystem engineers, tree cavity-creating and cavity-using birds. Within the context of African protected areas where tree felling by people is limited, the primary factors that prevent trees from reaching maturity are fire and elephant herbivory. A need for large, tall trees which have aged sufficiently to provide the necessary deadwood to facilitate excavation of cavities makes cavity-using birds potentially sensitive markers of habitat alteration (Newton 1994, du Plessis 1995, Monterrubio-Rico and Escalante-Pliego 2006). Deadwood accumulates slowly (Shackleton 1998), making it vulnerable to factors that preclude trees from ageing (Newton 1994, du Plessis 1995).

Bird species that use tree cavities comprise a major component of woodland vertebrate communities and perform a range of important ecological functions in many different biomes. They act as genetic linkers (Lundberg and Moberg 2003, Sekercioglu 2006) through seed dispersal and pollination; and primary cavity-users, like the bearded woodpecker (*Dendropicos namaquus*), are ecosystem engineers that create habitat (nests and roosts) for use by both avian and non-avian secondary cavity users. Habitat alterations that reduce cavity availability can affect the composition of entire species assemblages. For example, depletion of old-stand pine trees in Florida has increased competition between endangered red-cockaded woodpeckers (*Picoides borealis*) and other cavity-users, such as snakes and squirrels (Conner et al. 2001). Cavity-using birds, in addition to their more direct roles in seed dispersal, pollination and predation, thus influence trophic interactions indirectly (Gradwohl and Greenberg 1982).

At Chizarira National Park, in miombo woodland in north-western Zimbabwe, elephant densities over the past 30 years have tended to be high, at >1 km^{-2}, and at times as high as 3 km^{-2} (Cumming 1981, Dunham et al. 2006). Owing to the effects of elephants and the associated influence on fire regimes, these densities have affected tree distribution within the park, with the majority of trees in the matrix being either converted (and hence too short for most cavity-using birds), or too young (thus lacking deadwood content) to provide roosts and nesting possibilities for cavity-using birds.

In this study, I tested the hypothesis that large, nutrient-rich termitaria in a dystrophic savanna system can contribute to ecosystem resilience by providing refugia for key functional elements (i.e., woody plant

species) as matrix quality declines. More specifically, I tested whether large termitaria support a higher diversity of cavity-making and cavity-using birds in an elephant-impacted miombo woodland in Chizarira National Park. The study progressed in two steps. First, I investigated whether the preferred habitat for cavity-using birds (tall trees > 6 m, cavities, and trees with deadwood) occurred at higher densities on termite mounds. I then examined the relationship between suitable habitat (mounds, tall trees > 6 m, cavities, and trees with deadwood), and species richness and abundance of cavity-using birds.

Methods

Study area

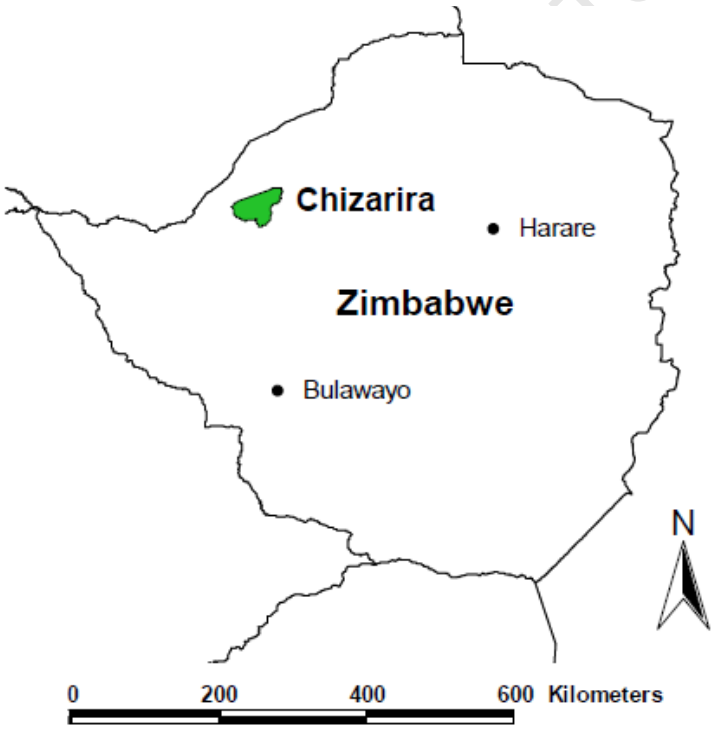


Figure 6.1. Area of study, Chizarira National Park (17°42´S, 27°55´E)

This study was carried out in the miombo woodlands of Chizarira National Park in north-western Zimbabwe during October-November 2007 (the bird breeding season) and April-May 2009 (non-breeding season). The area experiences a wet season from November to April, a cool dry season from May to July and a hot dry

season from August to November. Mean annual temperature is 20 - 22.5°C (maxima: October 32.5-35°C, July 22.5-25°C; Torrance 1965). Mean annual rainfall is 600 mm-800 mm (annual coefficient of variation of 25-30%; Lineham 1965).

Miombo is a broad-leaved deciduous woodland dominated by the Caesalpinioideae genera of *Brachystegia* and *Julbernardia* (White 1983). In many parts of south-central Africa, miombo woodland is characterized by massive vegetated termitaria up to 9 m high and 30 m in diameter at the base (Malaisse 1978). These termitaria form nutrient rich hotspots (Frost 1996) with higher small vertebrate biodiversity (Fleming and Loveridge 2003) on mounds than in the surrounding, generally dystrophic woodland (Huntley 1982). Chizarira is dominated by such mounds, constructed by *Macrotermes* (Isoptera, Macrotermitidae) termites. The impacts of elephants and fire have transformed most of the park's former tall, open woodland to shrubland (Cumming 1981) comprised mainly of regenerating *Brachystegia boehmii* and *Combretum* species in the matrix, with tall trees being confined to termitaria (fig. 6.2).

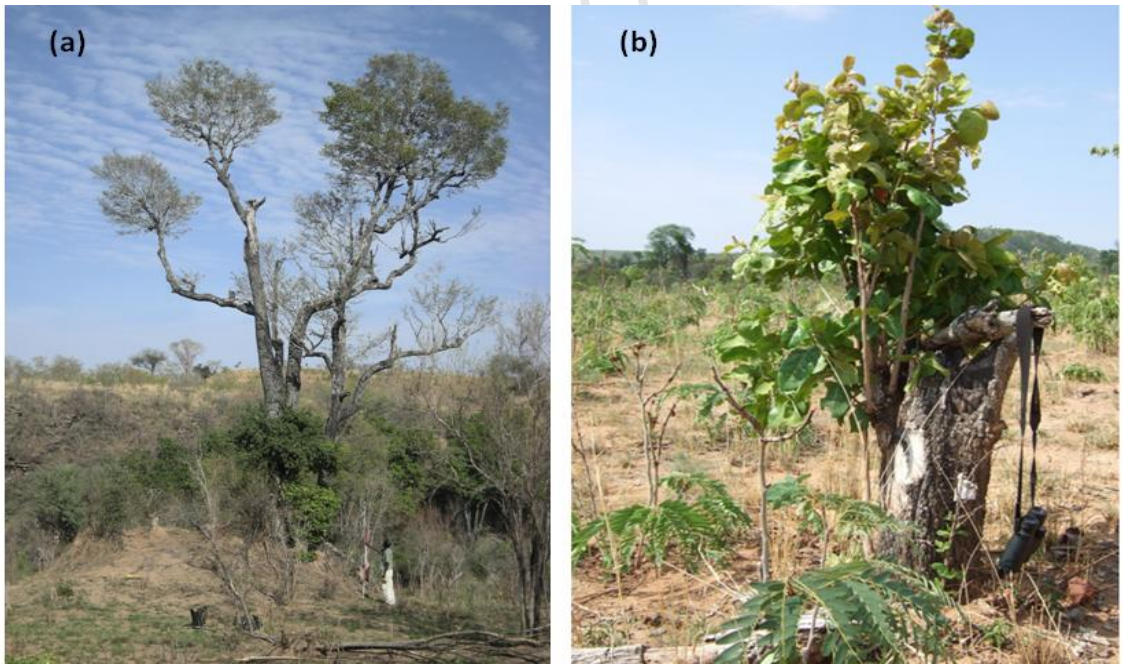


Figure 6.2. Typical woodland scene with a mound harbouring large trees (a). The short stature of converted trees in the matrix (a converted *Diospyros kirkii* in this example) is highlighted by a comparison for scale with the length of a binocular strap (b).

Field Methods

To determine whether termitaria provide additional habitat relative to the surrounding woodland matrix, I established 11 plots of 100 x 200 m^2. Mean mound density in the study site was 2 mounds ha^{-1}. There were 48 mounds on the 11 plots. I compared 48 pairs of mound and matrix sites (within these plots) for density of tall trees, density of trees with deadwood, and cavity density in the summer breeding season (fig.6.3). The sampling design was repeated in the non-breeding season for 14 different plots containing 54 mounds and matched matrix sites.

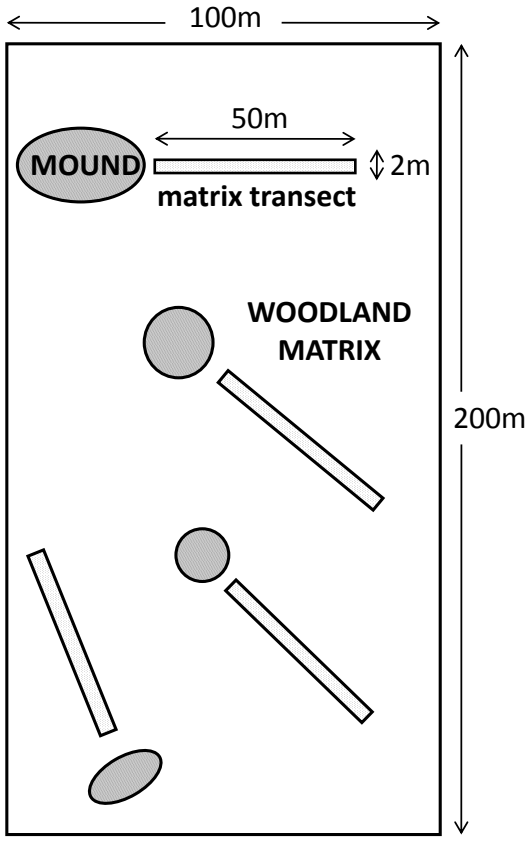


Figure 6.3. Representation of a hypothetical 2ha plot. Each mound was compared with an adjacent matrix transect for density (ha^{-1}) of cavities, tall trees > 6m, and trees with deadwood.

Within each plot I recorded the length, breadth, height and position of termite mounds >2m tall or >10m wide. Mound surface area was approximated by treating the shape as a cone. Each mound was compared to an adjacent matrix plot measuring 2 by 50 m^2 (0.1 ha). I elected to use linear transects to best represent overall tree structure in the matrix and capture the overall impact of elephants on trees, as their impact might be influenced by proximity to mounds (Anderson and Walker 1974, Levick et al. 2010). Matrix plots were set along randomly chosen compass bearings radiating out from the mound, starting 5 m from the perimeter of the mound. For each mound and matrix plot, counts for trees, cavities and trees containing deadwood were performed.

Cavity-using bird species are limited by availability of suitable tree cavities (Newton 1994). Trees with diameters at breast height (DBH) <15cm do not afford good roosting or shelter (Waters et al. 1990). Preferred cavities occur at higher elevations within trees (limiting attention from terrestrial predators; Nilsson 1984). A preliminary survey of 20 trees (of differing species) shorter than 6m showed no worn cavities. Thus only trees >6m in height and with DBH >10cm were considered. Species, height and DBH were noted. Cavity availability increases with age and size of trees, as these factors expand the quantity of deadwood that facilitates cavity formation (Newton 1994, du Plessis 1995).

I sampled cavity-creating and using birds using a point-count method (Thomas et al. 2002). Point counts were in a grid of 15 points (three rows of five points), spaced 150 m apart. Grids in which birds were sampled were centred on smaller 2 ha plots (for which habitat data were collected as described above) representative of the surrounding habitat within each grid, in terms of mound density and woody plant structure. At each point, species richness, abundance and distance from point of observation were recorded for cavity-creating and cavity-using bird species in a 75m radius over 10 minutes (Herremans 1995). All individual birds noted to have been in a previous count, and any birds that posed uncertainty in this regard, were not counted. Counts were undertaken during the first three hours following sunrise when birds were most active.

Data Analysis

Habitat variables

To test whether vegetation structure differed between termitaria and the matrix in terms of densities of trees greater than 6m in height, cavities and trees with deadwood, I used generalized linear mixed-effects models (assuming a Poisson distribution and log link function; function lmer in package lme4, program R 2.11.0, R Development Core Team 2010). The sampling pairs (mounds and corresponding matrix strip) were nested within the 2ha plots. Thus I nested mounds within plots, which were set as random variables, and I corrected for differences in area sampled using the logarithm of area as an offset in all models.

Evaluation of cavity-using bird sample-size

Relative species richness and abundance were calculated for bird assemblages at each of the 11 plots of equal sampling area. This was repeated for the 14 non-breeding season plots. I compiled sample-based rarefaction curves for each set of point count data, i.e., 2007 and 2009 using EstimateS (Colwell 2006). I used the nonparametric Incidence Coverage Estimator (ICE) and Michaelis–Menten richness estimate to evaluate sample-size adequacy (Colwell and Coddington 1994). When ICE and Michaelis-Menten richness values converge closely at the highest observed values, sampling can be considered sufficient (Longino et al. 2002).

Evaluating the effect of habitat on cavity-using bird species richness and abundance

I first tested for a correlation (using Spearman's Correlation Coefficient) between bird species richness and abundance with the habitat variables (mounds, tall trees, trees containing deadwood, and cavities) for each plot.

To assess how bird species richness and abundance varied with aspects of habitat (i.e., mounds, tall trees, trees with deadwood, and cavities within each plot), and whether the influence of these aspects varied between breeding and non-breeding season, I used generalized linear models (Poisson error distribution, log link function) implemented via the glm function in the program R 2.11.0. For this analysis the unit of replication was the plot, as bird data were collected at this level. The four habitat variables (number of trees greater than 6m in height, cavities, trees with deadwood, and number of

mounds) were now explanatory variables and I was interested in their relative ability to explain the patterns in bird species richness and abundance.

Since these habitat variables were correlated with each other, I fitted them one at a time in four separate models. I then used model selection based on corrected Akaike's Information Criterion (AIC, Burnham and Anderson 2002) to rank the models and to examine their relative ability to explain the pattern in the data. I used corrected AICs because I had a relatively small sample size (Hurvich and Tsai 1989). Season and its interaction with the respective habitat variable were always included in the model to account for potential effects of seasonality.

Results

Habitat variables

All habitat components that are considered important for cavity-using birds were found in significantly higher densities (ha^{-1}) on mounds than in the matrix. Density of trees > 6 m in height was nearly 10 times higher on mounds than in the matrix (table 6.1). The incidence of trees with deadwood was also nearly 10 times greater on mounds, and the density of cavities was just over nine times as high on mounds as in the matrix (table 6.1).

Woody species composition differed between mound and matrix: appendix 6.1 lists the woody species that were found on >80% of plots. Functionally, the species assemblages on mounds and matrix seem to be quite different, with 67% of species found on mounds having bird dispersed fruits, compared to only 39% of species in the matrix.

Table 6.1. Generalized linear mixed-effects models showed that the favoured habitat of cavity-using birds (trees > 6 m in height, trees with deadwood and tree cavities) all occurred at significantly increased densities (ha^{-1}) on mounds. The random effects were mound-matrix pair nested within plots. The p values given for the matrix rows indicate whether these values are significantly different to zero, and the p values given in the mound rows indicate p values for difference of mounds from matrix plots.

Fixed effects:	**Estimate on log scale**	**Std. Error**	**Z value**	**P**	**Matrix (mean/ha)**	**Mound (mean/ha)**
Trees > 6m in height						
Matrix	1.7645	0.3122	5.653	<0.001	5.8	
Mound	2.2441	0.3162	7.096	<0.001		55.1
Trees with deadwood						
Matrix	-0.1198	0.6488	0.185	0.854	0.9	
Mound	3.4971	0.6543	5.345	<0.001		8.8
Tree cavities:						
Matrix	0.1315-	0.4020	0.327	0.744	0.9	
Mound	4.5901	0.3698	12.412	<0.001		8.3.

The effect of habitat on cavity-using bird species richness and abundance

I recorded 64 cavity-using birds representing 21 species in the 11 breeding season plots and 190 birds from 20 species in the 14 non-breeding season plots (appendix 6.2). Michaelis-Menton and ICE estimators converged closely for the sample-based species rarefaction curves, indicating sufficient sampling (breeding season $S = 6.2629A^{0.5226}$; non-breeding season: $S = 5.8548A^{0.4492}$, where S = number of species observed and A =

number of plots sampled. Of these cavity-using bird species, nearly 60% included fruit in their diets and just over 40% were nectarivorous (Hockey et al. 2005, see appendix 6.2).

Table 6.2. Spearman Rank pair-wise correlation coefficients (r –values) showed that many of the habitat variables were correlated with each other (c-u = cavity-using; numbers in brackets indicate mean ± standard deviation).

Breeding Season n = 11 plots						
variable:	c-u bird richness	c-u bird abundance	mounds	trees	dead-wood	cavities
c-u bird spp. richness (5.8 ± 3.3)	1.00					
c-u bird abundance (10.6 ± 7.8)	0.89*	1.00				
mounds (4.4 ± 2.2)	0.65*	0.77*	1.00			
trees (47.4 ± 49.7)	0.32	0.38	0.44	1.00		
deadwood (2.4 ± 2.8)	0.72*	0.85*	0.68*	0.47	1.00	
cavities (20.6 ± 22.4)	0.82*	0.83*	0.78*	0.29	0.80*	1.00
Non-breeding season n = 14 plots						
c-u bird spp. richness (5.9 ± 2.5)	1.00					
c-u bird abundance (13.8 ± 7.9)	0.82*	1.00				
mounds (3.6 ± 1.7)	0.84*	0.69*	1.00			
trees (8.14 ± 4.6)	0.79*	0.61*	0.68*	1.00		
deadwood (6.4 ± 3.9)	0.82*	0.72*	0.62*	0.93*	1.00	
cavities (33.1 ± 22.9)	0.69*	0.53	0.66*	0.88*	0.88*	1.00

** $p < 0.05$*

Many of the habitat variables correlated with each other (table 6.2). In the breeding season, bird species richness and abundance were significantly positively correlated with number of mounds, amount of deadwood and cavities, but were not significantly correlated with density of trees > 6 m in height. In the non-breeding season, bird species richness and abundance were significantly positively correlated with number of mounds, number of trees > 6 m in height, and amount of deadwood. Although species richness correlated with cavities, bird abundance did not (fig. 6.4).

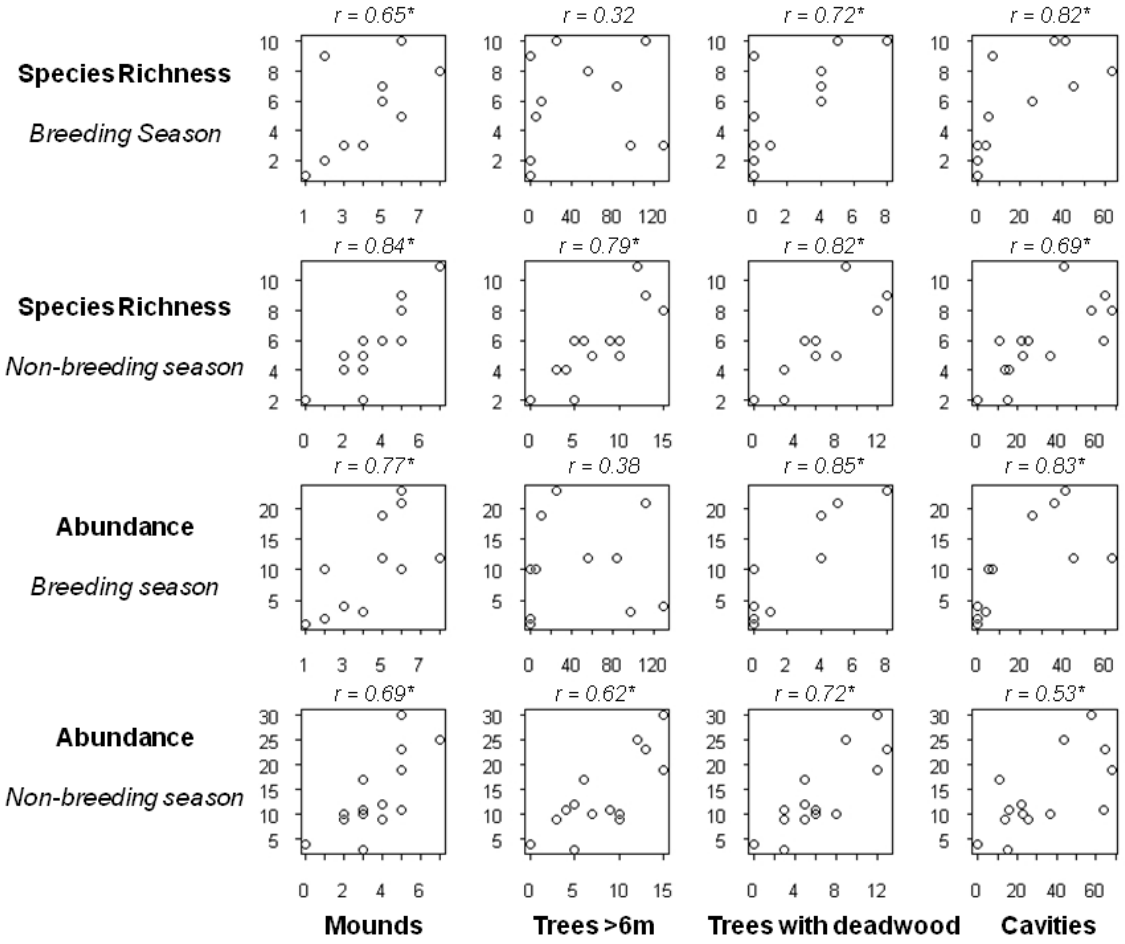


Figure 6.4. Scatterplots showing correlation (Spearman Rank) between cavity-using bird species richness, cavity-using bird species abundance, and the habitat variables across seasons for the 2 ha plots. The x-axes values for all graphs in column 1 are number of mounds; column 2, trees > 6m; column 3, trees with deadwood and column 4, cavities (*denotes $p < 0.05$).

For both cavity-using bird species richness and abundance, inclusion of the number of trees with deadwood resulted in models with the lowest AICc value, suggesting that the presence of deadwood is the best predictor of bird species richness and abundance (table 6.3). For species richness, however, the model with the number of mounds per plot was equally well supported by the data.

Table 6.3. Results of model selection procedure to examine how bird species richness and abundance co-varied with habitat features.

Response variable	Terms in the model	Number of parameters	Maximised log likelihood	ΔAICc	Akaike weights (w_i)	Deviance explained by the model
Cavity-using bird species richness						
Model 3 (Best model)	Season × Number of trees with deadwood per plot	4	-51.97	0	0.4497	52.9%
Model 1	Season × Number of mounds per plot	4	-52.08	0.2	0.4011	52.3%
Model 4	Season × Number of cavities per plot	4	-53.11	2.3	0.1432	46.4%
Model 2	Season × Number of trees >6m per plot	4	-56.37	8.8	0.0055	27.9%
Model 5	Season	2	-61.28	12.6	0.0002	0.002%
Abundance of cavity-using birds						
Model 3 (Best model)	Season × Number of trees with deadwood per plot	4	-72.41	0	9.99×10^{-1}	66.74%
Model 1	Season × Number of mounds per plot	4	-82.26	19.70	5.27×10^{-5}	51.15%
Model 4	Season × Number of cavities per plot	4	-86.42	28.01	8.26×10^{-7}	44.57%
Model 2	Season × Number of trees >6m per plot	4	-93.80	42.78	5.12×10^{-10}	32.87%
Model 5	Season	2	-112.08	73.32	4.38×10^{-17}	3.95%

Discussion

In the miombo woodland of Chizarira National Park, termitaria and their associated vegetation emerge as important refugia for cavity-using birds. This relationship holds for both the breeding and non-breeding seasons. The primary habitat components for cavity-using birds (tall trees, cavities and trees with deadwood) are concentrated on termite mounds within the system.

In plots with more mounds, tall trees, cavities, and trees with deadwood, greater species richness and abundance of cavity-using birds was observed. The best model fit for both cavity-using bird species richness and abundance was number of trees with deadwood, explaining 52.9% and 66.7% of deviance

for species richness and abundance, respectively. My analyses indicate that the processes and mechanisms that drive the observed association between mounds and cavity using birds involve not only the persistence of favourable habitat, but specifically the presence of deadwood, which is found predominantly on old, senescing, tall trees.

I sampled cone-shaped areas of mounds, but long, thin transects in the matrix to assess tree density and structure. These differences in shape of sampling areas could have introduced bias: the possibility exists that comparing patches using narrow transects does not capture the thinning that might result from competition (since no tree on a mound was ever 50 m away from any other tree on the same mound), and that competition might have led to fewer large trees on mounds. However, this effect would make my sampling technique more rather than less prone to Type II errors, and I still found significantly more large trees on mounds. Aerial photographs of the study area support the position that the lack of tall trees in the matrix is unlikely to be an artefact of a long, thin transect, as they confirm that very few large trees remain in the matrix.

Cavity-creating and cavity-using birds need deadwood. Aside from being the preferred medium for excavators (du Plessis 1995), deadwood is also a very important source of invertebrate food (the larvae and pupae of beetles, especially Cerambycidae and Buprestidae;Tarboton 1970, Short 1971) for many species of primary cavity-using birds. Such trees occur at greater densities on termitaria in this system. The persistence of both tall trees and trees with deadwood on termite mounds involves a complex set of feedbacks that follow from the combined actions of termites, elephants and the cavity-using birds themselves.

Factors leading to persistence of trees with deadwood within the system

The engineering effects of *Macrotermes* termites influence the distribution of tall trees in the system. The relatively eutrophic soils of termitaria facilitate establishment and growth of a unique and different suite of trees relative to the matrix (Fleming and Loveridge 2003). Termitaria protect these trees against the effects of both elephants and fire, through a number of mechanisms. Soils on termitaria have a higher moisture content than the surrounding matrix soils (Dangerfield 1991), offering partial protection from the effects of fire

(Harrington 1991). Termitarium height limits exposure to fire by elevating mound vegetation above that of the matrix. Within the study site, most mounds were surrounded by a large halo (often many metres in width) of eroded soil that supports far less vegetation than the surrounding matrix, and may act as a natural firebreak. Edkins et al. (2007) showed that elephant browsing on baobabs (*Adansonia digitata)* was less apparent on steep slopes in the Kruger National Park, South Africa, probably because these trees were relatively less accessible. The steep sides of some large termitaria appear to us to provide similar protection, although I do not currently have data to support that claim.

The tall trees that remain on termitaria are able to senesce, and this in turn provides the necessary deadwood for primary cavity-users to fashion into cavities not only for their own roosting and nesting, but also for use by secondary cavity-using birds. Deadwood is important habitat for many invertebrates favoured in the diets of primary cavity-using birds. The consequent increase in avian activity on such mound-associated trees is itself likely to play an important role in the maintenance of structure on termitaria, as birds bring in seeds and nutrients from both the matrix and further afield. For example, many of the tree species on termitaria produce bird-dispersed fruit (Fleming and Loveridge 2003; this study), and I found that nearly 60% of the cavity-using birds observed include fruit in their diets (see appendix 6.2; Hockey et al. 2005). Thus, the activities of cavity-using birds also increase the likelihood of recruitment of seedlings, influencing the composition of trees on mounds and ultimately the maintenance of tall, dense, and old trees.

The different composition of plant species on mounds relative to the woodland matrix may be of little consequence in times of infrequent fire and low herbivore impact. However, when elephant densities are high, with associated increases in grass cover relative to woody cover so that fires are more intense, termitaria appear to make a valuable contribution to the resilience of Chizarira's miombo woodland by acting as islands or refugia for tall, old trees and thus for cavity-using birds. The consequences for the ecosystem are important; termitaria maintain valuable ecological processes that are linked to the presence of cavity-using birds. The cavity nesters in this study were not only dominated by frugivores, but almost 40% of them are also nectarivorous (appendix 6.2). Genetic linkage through seed dispersal and pollination influences the recruitment

of many plant species (Keller and Waller 2002). In making cavities, primary cavity-users, like the bearded woodpecker (*Dendropicos namaquus*), engineer habitat (nests and roosts) for some species of secondary cavity users (du Plessis 1995, Martin and Eadie 1999). Thus the presence of woodpeckers and barbets could be important for the persistence of starlings, parrots, kingfishers, hornbills, rollers, flycatchers, swallows, owlets, tits, scimitarbills, sparrows and wood-hoopoes (see appendix 6.2. for nomenclature) as well as other vertebrates like the tree squirrel (*Paraxerus cepapi*) and cavity-using reptiles. As these species include insectivores, frugivores, granivores and omnivores, the consequences of habitat alterations that reduce cavity availability could be expected to affect not only the composition of cavity users, but the entire food web at a range of trophic levels.

This study shows that termite mounds can play a major role in providing refugia and sustaining biodiversity in disturbed landscapes. The interaction between large, nutrient-rich *Macrotermes* mounds (which foster a different set of woody plant species relative to the matrix), cavity-using birds and the combined effects of elephant herbivory and fire, has led to increased heterogeneity within the woodland. As forage availability in the matrix diminishes, the obvious question that emerges is whether, or at what point, current levels of fire and herbivory will overwhelm the buffering capacity of the termitaria, leading to a landscape not only lacking in tall trees and cavity-using birds, but with far reaching consequences for regional biodiversity as trophic relationships alter.

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Appendices

Appendix 6.1. List of tree species that occurred on 80% of sites. Nomenclature follows Coates Palgrave (2005).

Family-Subfamily	Zimbabwe Tree number	Species	Bird dispersed fruit?
Mound & Matrix			
Fabaceae-Caesalpinioideae	246	*Colophospermum mopane*	0
Combretaceae	775	*Combretum molle*	0
Fabaceae -Papilionoideae	360	*Xeroderris stuhlmannii*	0
Matrix			
Annonaceae	110	*Friesodielsia obovata*	1
Fabaceae-Caesalpinioideae	248	*Brachystegia boehmii*	0
Fabaceae-Caesalpinioideae	252	*Brachystegia spiciformis*	0
Fabaceae-Caesalpinioideae	260	*Julbernardia globiflora*	0
Fabaceae-Papilionoideae	348	*Dalbergia melanoxylon*	0
Fabaceae-Papilionoideae	355	*Pterocarpus rotundifolius*	0
Fabaceae-Papilionoideae	357	*Philenoptera violacea*	0
Euphorbiaceae	445	*Pseudolachnostylis maprouneifolia*	1
Euphorbiaceae	474	*Bridelia cathartica*	1
Anacardiaceae	538	*Lannea discolor*	1
Combretaceae	766	*Combretum apiculatum*	0
Combretaceae	781	*Combretum zeyheri*	0
Combretaceae	785	*Terminalia brachystemma*	0
Combretaceae	792	*Terminalia stenostachya*	0
Ebenaceae	855	*Diospyros kirkii*	1
Rubiaceae	1056	*Crossopteryx febrifuga*	1
Rubiaceae	1067	*Catunaregam taylori*	1
Combretaceae	no number	*Combretum collinum*	0
Mound			
Olacaceae	92	*Ximenia americana*	0
Capparaceae	128	*Capparis tomentosa*	1
Capparaceae	149	*Maerua prittwitzii*	1
Fabaceae-Mimosoideae	216	*Acacia nilotica*	0
Fabaceae-Caesalpinioideae	267	*Cassia abbreviata*	0
Euphorbiaceae	446	*Flueggea virosa*	1
Anacardiaceae	540	*Lannea schweinfurthii*	1
Rhamnaceae	620	*Berchemia discolor*	1
Combretaceae	772	*Combretum hereroense*	0
Combretaceae	776	*Combretum mossambicense*	0
Sapotaceae	843	*Manilkara mochisia*	1
Ebenaceae	847	*Euclea divinorum*	1
Ebenaceae	857	*Diospyros mespiliformis*	1
Ebenaceae	859	*Diospyros quiloensis*	1
Ebenaceae	860	*Diospyros sinensis*	1

Appendix 6.2. Cavity-using bird species list at point counts, Chizarira National Park.

Nomenclature follows Hockey et al. (2005). Frugivores marked with an asterisk are those that have been observed behaving in ways that could disperse fruit seeds.

Robert's Number	**Species (Common name, S*cientific)***	**Frugivore**	**Nectarivore**
364	Parrot, Meyer's *(Poicephalus meyeri)*	1	0
398	Owlet, Pearl-spotted *(Glaucidium perlatum)*	1*	0
437	Kingfisher, Striped *(Halcyon chelicuti)*	0	0
447	Roller, Lilac-breasted *(Coracias caudatus)*	0	0
448	Roller, Racquet-tailed *(Coracias spatulatus)*	0	0
452	Wood-hoopoe, Green *(Phoeniculus purpureus)*	1	1
454	Scimitarbill, Common *(Rhinopomastus cyanomelas)*	0	1
457	Hornbill, Grey *(Tockus nasutus)*	1	0
459	Hornbill, Southern Yellow-Billed *(Tockus leucomelas)*	1	0
463	Ground-hornbill, Southern *(Bucorvus leadbeateri)*	0	0
464	Barbet, Black-collared *(Lybius torquatus)*	1	1
473	Barbet, Crested *(Trachyphonus vaillantii)*	1	1
486	Woodpecker, Cardinal *(Dendropicos fuscescens)*	1	0
487	Woodpecker, Bearded *(Dendropicos namaquus)*	0	0
525	Swallow, Mosque (perched) *(Hirundo senegalensis)*	0	0
694	Flycatcher, Southern Black *(Melaenornis pammelaina)*	0	1
763	Starling, Meves's *(Lamprotornis mevesii)*	1	0
765	Starling, Greater Blue-eared *(Lamprotornis chalybaeus)*	1	0
766	Starling, Miombo Blue-eared *(Lamprotornis elisabeth)*	1	1
769	Tit, Southern Black *(Parus niger)*	1*	1
804	Sparrow, Southern Grey-headed *(Passer diffuses)*	1	1
805	Petronia, Yellowthroated *(Petronia superciliaris)*	0	1

7

Synthesis

Result summary

The results presented in this thesis demonstrate that spatial heterogeneity, in the form of *Macrotermes* termite mounds, influences woody plant assemblages, woody plant functional diversity, and a guild of birds that are intimately dependent on woody plants for provision of both roosting and nesting habitat. In exploring the contribution of soils, fire regimes, and herbivory, it presents a platform for understanding how such assemblages form and are maintained. Some of the main conclusions are as follows.

1) As soils of the dystrophic miombo woodland matrix become increasingly rich in clay and nutrients, and as termitaria enlarge, a progressive change in woody plant species occurs, as a product of both increased mound surface area and soil composition. By mound surface areas of only $10m^2$, the first species not resident to the general miombo woodland matrix begin to colonise the mound. As mounds enlarge further, and as soils become increasingly eutrophic, indicator species that characterise the matrix gradually disappear. Ultimately mound indicator species, characteristic of woody species beyond the miombo system, come to dominate, and the establishment of the mature assemblage shares similarities with savanna tree patch dynamics (with distinct phases of patch colonisation, patch resource dynamics and patch lifespan; 1994). Many of the mound species are well-represented in neighbouring riparian areas. The emergence of at least three distinct assemblages not only increases niches for other species; the inclusion of woody plant species from biomes beyond the woodland matrix adds to the diversity of species, with implications for resilience of the miombo woodland (see Chapter 2).

2) Communities that contain species with a variety of responses to disturbance are thought to be better buffered against environmental perturbation (Elmqvist et al. 2003, Folke et al. 2004). By comparing relative representation of response-related functional groups between mound and matrix habitats, it emerges that spatial heterogeneity associated with termitaria within a heavily elephant-impacted, dystrophic savanna woodland influences the functional traits represented within the woody plant community, and thus the system overall. In Chizarira, the relative abundance of species in different functional groups (particularly, those defined by their responses to fire and soil type) differed between mound and matrix. Mounds also added functional groups to the system. By harbouring species that

represent functional groups that differ from those in the matrix, the presence of termite mounds generates within the system a capacity to better handle disturbances, and provides an example of how fine-scale spatial heterogeneity that fosters alpha diversity can potentially influence the stability of the entire system (Chapter 3).

3) The combination of habitat heterogeneity, competition and disturbance can affect dispersal and colonization, and in so doing create diversity (Weiher and Keddy 1999). In African savannas heterogeneity in the form of *Macrotermes* termitaria is known to influence tree structure, harbouring woody plants of greater average height than those in the matrix (Joseph et al. 2011). Browsers and mixed feeders consistently have a negative impact on woody cover (as opposed to grazers, which can depress woody cover at low biomass, but above a certain threshold of grazer biomass, lead to increase in woody cover; Sankaran et al. 2008). Forty years of exposure to greater levels of browsing has altered both woody plant assemblages and lowered functional diversity of the woodlands in question. Spatial heterogeneity can influence disturbance regimes (Romme 1982, Turner 1987, Turner 1989), and in the vicinity of Lake Chivero, termitaria illustrate this by emerging as repositories of functional richness. For the system overall, functional evenness has been maintained despite lowered functional richness, demonstrating contraction of woody plant communities in trait space as similar functional types are lost across treatments. Such a pattern implies a loss of functional diversity and resilience in the face of browsing pressures (Chapter 4).

4) Although it has been shown that at finer scales local heterogeneity can add complexity to fire regimes, no studies have hitherto focussed on such effects in miombo woodland. By testing for a fire-sparing effect of large termitaria on woody vegetation structure and composition within a system that reflected its high elephant densities, it emerges that termitaria not only act as refugia for the trees that they harbour, but that these trees display very different adaptations to fire from those in the matrix. Nefabas and Gambiza (2007) showed that resprouting effort can be an adaptation to fire, and in Chizarira National Park it emerges that on-mound trees belong to an assemblage both less exposed to fire damage, and with lower resprouting vigour than observed for matrix species. Despite mound vegetation receiving greater attention and damage by herbivores than matrix neighbours, tall trees that are less adapted to fire are harboured on mounds. This unique suite of woody plants has previously been attributed to edaphic factors.

It now appears that fire-retardant properties of mounds (e.g., less grass, elevation above the fire line) also play a part. Termitaria allow a distinct assemblage of woody species that resprout poorly after fire to persist in a fire-prone matrix. Termitaria harbour habitat for cavity-using birds (Joseph et al. 2011), small vertebrates and arthropods, support preferred forage to certain herbivores (Holdo and McDowell 2004, Loveridge and Moe 2004, Mobæk et al. 2005); and ultimately increase primary, secondary and tertiary productivity (Pringle et al. 2010). Such fire-sparing is thus likely to have positive impacts at a range of trophic levels within the system (Chapter 5).

5) In testing the role that landscape heterogeneity can play in providing refugia and sustaining biodiversity in disturbed landscapes, it emerges that the mound-building activities of *Macrotermes* (Isoptera) termites can influence avian diversity. The nutrient rich islands that are termitaria house important habitat for cavity-using birds (tall trees, cavities and deadwood). In the context of heavy impacts on the miombo woodland by elephants and fire, termitaria act as refugia for cavity-using birds (harbouring greater species richness and abundance) and contribute to the resilience of a guild of birds through high on-mound densities of trees rich in deadwood. Large termitaria thus play a role in maintaining functionally important components of the avifauna that are important pollinators, genetic linkers, and engineers of habitat for other cavity-using taxa (Chapter 6).

It is well known that the Miombo, Africa's largest contiguous block of savanna woodland, has been placed under increasing threat from current commercial and agricultural trends (Campbell 1996). What has been less appreciated is the pressure on this ecologically important woodland even within reserves, which by necessity of population pressures and land-use practices, have come to behave increasingly like islands. This project was initiated to better understand the influence of termitaria on disturbance regimes (herbivory and fire), biodiversity, and functional diversity in miombo woodlands surrounded by anthropogenic boundaries. My interrogation of the extent to which landscape heterogeneity in the form of large termitaria influences woody plant and avian diversity in disturbed landscapes has shed new light on the interplay between nutrient rich patches and disturbance regimes, the effects of which are likely to become increasingly more pronounced by current population trends and land use practices in adjacent communal farmlands.

Termitaria as foci for species and functional diversity in disturbed and dystrophic savanna woodlands

Dystrophic savanna systems (with soils and vegetation low in nutrient content) interspersed with islands of nutrient-rich patches, have provided an ideal study site for demonstrating the contribution of fine-scale spatial heterogeneity to more general (and broad scale) ecosystem function. Termitaria, by providing refugia for key functional elements within the system, sustain both biodiversity and functional diversity in landscapes disturbed by elephant, browsing herbivores and fire. By returning to first principles, and considering biodiversity as being composed of composition, structure and function (Franklin et al. 1981), nested into levels of organization that encompass different spatio-temporal scales: regional landscape, community ecosystem, population-species and the finer genetic level (Noss 1990), the impacts of large termitaria can be observed across a range of scales.

Although the above-ground area of large termitaria in this study comprises less than 5% of the total habitat surveyed, the foraging activity of *Macrotermes* involves the majority of the woodland matrix surface area (and includes an extensive below-ground component). As a consequence of nutrient concentration from an already dystrophic matrix, soils on termitaria (as patches that interact directly with their surrounds through ongoing termite activity) become increasingly eutrophic as mounds enlarge. At the finer scales of biodiversity (genetic and species level), enriched soils exclude many miombo trees and create a niche for a very different suite of species, many of which are structurally, functionally and phylogenetically different from those in the surrounding woodlands. Change occurs even at relatively small mound surfaces areas, and is marked by the emergence of a number of distinct assemblages that, although probably part of a continuum in the growth in size and alteration of soil properties on mounds, increase habitat heterogeneity. The families Ebenaceae and Capparaceae are well represented on mounds, whilst Anacardiaceae, Bignoniaceae, Boraginaceae, Olacaceae, Rhamnaceae, Sapotaceae, Solanaceae occurred only on mounds at certain sites. Fabaceae (notably the subfamily Caesalpinioideae), and Combretaceae characterized the matrix. Termitaria also influence the distribution of woody plant functional traits and functional groups within the system. Trees on termitaria bear leaves with higher specific leaf area and palatability that are richer in micronutrients (nitrogen and phosphorous). Being favoured by herbivores within the system, they undergo greater herbivore damage. Despite this, they grow

taller than matrix species. In addition, mound-associated trees are fruit-bearing, evergreen, and often house species characteristic of riparian assemblages. This in turn influences diversity of other taxa. Cavity-using birds are one example (attracted by structure and deadwood); another is the tree squirrel *Paraxerus cepapi*, a species which is generally absent from miombo woodlands (Skinner and Chimimba 2005), and restricted almost exclusively to mounds in my study sites.

Once established, the differences in soils and woody plants are maintained not only by ongoing termite activity. Attention from cavity-using and frugivorous birds and mammals, and herbivores, add further micronutrients and propagules that facilitate the process. Even the effects of trees themselves, which can influence competition and spatial arrangement of other plants through shade and root effects (eg. nutrient and water distribution), enhance change over time. Given the well documented adaptations of plants, and the changes to soil composition, in the setting of the disturbance regimes of fire and herbivory, these too are likely to contribute to maintenance of the status quo (consider for eg. plant spinescence and decreased palatability in the face of herbivory; or the effect of fire on the concentration of soil micronutrients like nitrogen). That mound species have smaller seeds (which in general disperse over greater area, in greater numbers), supports the observation that such species are often derived from propagules with a distant source of origin. The dystrophic matrix is characterized by ectomycorrhizal species, which probably provides a competitive advantage in a phosphorous-poor milieu. Matrix trees have larger seeds (a possible adaptation to lower nutrient soils, as large seeds imply greater investment in establishment and survival), and are better resprouters post fire, reflecting their increased exposure to fire. Considered within the context of their great age, size, and broad distribution within miombo systems (Watson 1967, Malaisse 1978, Millington et al. 1994), the influence of *Macrotermes* termites extends over many thousands of square kilometres to beyond regional ecosystems and to include landscape level effects. The fire-sparing effect of mounds at smaller scales (CNP) affects the distribution of woody species, and maintains fire-sensitive species within the system. Their influence on fire at larger scales remains untested, but the potential to impact upon fire regimes over vast areas of south-central Africa that contain miombo and large termitaria exists. Termitaria provide preferred forage for herbivores (and thus can influence the distribution and feeding habits of herbivores at a regional scale). This, coupled with the mound-associated maintenance of functional richness in the face of heavy grazing (functional richness

declined as exposure to grazers increased, but was nevertheless higher on mounds), further emphasises the ecological contribution of termitaria to rangelands throughout the system. Through foraging, and by influencing the distribution of animals and plants, termites impact on nutrient cycling. They affect genetic linkage and the distribution of predator and prey species (for e.g. different cavity-using species, and certain invertebrates associated with deadwood) both directly and indirectly. In impacting upon biodiversity, functional diversity and disturbance regimes, *Macrotermes* mounds at the landscape level can be expected to have effects on processes across a broad range of trophic scales that ultimately shape productivity within the miombo system.

Recommendations for future management

Important applications of this research to conservation efforts emerge in the context of current pressures facing miombo woodlands throughout south-central Africa. Confronted with burgeoning regional human populations (Cohen 2003), it stands to reason that reserves and national parks will be increasingly forced to limit the movement of herbivores. Add to this the ongoing requirement of people for additional agricultural resources (Sileshi et al. 2007), and the identification of patterns and processes that harbour biodiversity and potentially add resilience to a given system becomes increasingly relevant. Termitaria within miombo systems that are heavily impacted by herbivores play an important role in creating and maintaining niches that foster both functional diversity and biodiversity. Although this study spanned only four field years (2007-2011), the study sites have well-documented herbivore histories that range from three decades (and beyond) for sites within Chizarira National Park, to forty years for the sites abutting on Lake Chivero. Some valuable points for management emerge from my study.

1) The identification of biodiversity hotspots (Myers and Mittermeier 2000), albeit at a fine scale, has important implications for optimizing conservation management decisions. *Macrotermes* termitaria, as seats of both functional diversity and biodiversity, deserve special attention both within reserves and throughout the miombo woodland network. This poses challenges to the ongoing 'chitimene' agriculture approach, in which termite soils and burned boughs of trees are used to enrich cropland soils (Frost 1996), and also to the practice of harvesting of large trees found on mounds (in their entirety) for wood. Although

these activities allow termitaria and miombo trees to furnish an ecosystem service for local farmers, unless sustainable approaches that focus on preserving the woody structure enhanced by the presence of termitaria (eg. provision of shade trees/subcanopy microclimate/wood harvesting) are explored, centuries old foci of biodiversity will be lost (fig. 7.1).

Figure 7.1. Comparison of a mound within Chizarira National Park (left) with one in the adjacent communal lands (right).

2) Studies in South African savannas have demonstrated links between savanna degradation and higher production costs, poor understanding of grazing strategies, loss of subsidies to farmers, altered fire regimes and subdivision of agricultural sites into units that have lost their economic viability (Seymour and Milton 2003). Benzie (1986) showed that termite densities increased in fire-protected plots over a 2 year period, probably due to increased food supplies. It is likely that fire itself would also have a direct impact on termite populations. Although this is a very different system, with different farming techniques in place, given the value of termitaria to regional biodiversity and the potential cascade of loss that might be associated with their disappearance, a concerted approach to maintain their existence is desirable. In particular, adoption of regional fire-management strategies that aim at both replicating natural frequencies within reserves, but which also focus on educating small-scale farmers to the potential effects of over-frequent burning to the long-term sustainability of ecological processes is to be encouraged.

3) Reserves, even those of very large area, are nevertheless unnatural systems. Browsing of ungulates in a confined area can have an effect on both woody plant assemblage and functional diversity. Loss of function is never desirable within a reserve, but the solutions are equally difficult to imagine. My finding of a 'functionally thinned' woodland system on the banks of Lake Chivero as a consequence of ongoing browsing pressures over four decades suggests a need for rest/respite from herbivory if regeneration and succession of typical miombo species is to be achieved. Reserves divided into camps where wild ungulates are rotated like domestic stock is not a solution palatable to most managers, and certainly not one to be invited by the tourism industry. Imaginative managerial approaches are awaited in the context of limited land availability.

4) The existing fire regimes within Chizarira National Park have all but converted the miombo woodland to shrubland and grassland. This has had obvious implications for the miombo woodland, which has thinned in the face of a combination of high elephant densities and associated dry-season fires. The key issue here can be resolved by management decisions. The obvious and ethically agreeable solution is a re-establishment of the historic corridors that permitted the free movement of elephant into the Zambezi Valley and surrounding woodland areas (for e.g. Chete). However, this option will need a high degree of community goodwill and co-operation, as the competition between humans and elephants for miombo resources in an economically impoverished region is intense. A more controversial solution involves the active control of elephant numbers, and no euphemisms can soften the concept of culling. This option is difficult to sanction in a continent that over the last few centuries has lost perhaps 95% of its elephant population. Personal observation over the past months suggest to me that the discussion is currently inappropriate (for Chizarira, at least), as I have witnessed a rapid dwindling in elephant numbers, to the degree that the herds of 50 or more elephant observed only four years ago, are now no longer extant. In fact, on my last visit, I witnessed rapid regeneration of *Brachystegia* throughout the park, and only scattered and skittish elephant (fig. 7.2). Similar findings have been noted by Dunham (2008): a survey of the area showed a 16 fold increase in carcasses through anthropogenic mortality, and a rise in carcass ratio (number of carcasses as a percentage of total population) from 1.25% in 1989 to 15.4%.

Figure 7.2. A regenerating *Brachystegia boehmii* woodland in Chizarira (a); the majority of trees are resprouting post coppicing (b).

However, the issue remains: as elephant, forced to congregate at ever-increasing densities within reserves, open woodland canopies, the consequent increase in grass biomass can lead to the hotter fires. A likely consequence is ongoing conversion of the remaining woodland to grassland. This switch has obvious implications for diversity in systems that are already under threat, and remains perhaps the most difficult management issue at hand.

As I watch the miombo regenerate in the absence of elephant, it dawns on me that the most important studies are yet to come. The first, already mentioned in chapter 6, addresses the need to evaluate the point at which fire and herbivory might overwhelm the buffering capacity of termitaria with regard to maintenance of biodiversity, as forage availability in the matrix diminishes. A landscape depleted of tall trees, cavity-using birds, and with a lowered functional diversity can be expected to have far-reaching consequences for regional biodiversity as trophic relationships alter. The second is current, and in the context of regional alteration of woodland and woody species in prominent reserves like the Chobe (Ben-Shahar 1998),

Hwange (Holdo 2003) and Kruger (Eckhardt et al. 2000), Chizarira (with its recent depletion of elephant numbers) offers the researcher a unique opportunity to grapple with a very important and topical question: how does a woodland regenerate in the wake of such heavy impact? I suspect that a closer look at the effects of regeneration on biodiversity will have much to offer conservation managers and strategists, at a time when decisions are expected to optimize not only the future biological potential, but also the budgetary constraints of areas under management.

Implications of my findings for ecosystem resilience remain untested, but in the setting of increased functional and species diversity, it appears that the presence of termitaria allows the system to maintain processes and structure in the face of perturbation by fire and herbivory, *sensu* Holling (1973) and Walker et al. (2006). Communities with a variety of responses to disturbance can be better buffered against environmental perturbation (Chapin 2003, Elmqvist et al. 2003, Folke et al. 2004); and harbouring species that represent response functional groups different to the matrix connotes a system better equipped to handle disturbances. In closing, it appears that the eutrophic soils of *Macrotermes* termitaria hold fertile ground for future research.

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